A testate amoeba-based transfer function for paleohydrological reconstruction from boreal and subarctic peatlands in northeastern Canada

A. Lamarre, G. Magnan, M. Garneau, É. Boucher

Peatland Ecosystems Dynamics and Climatic Change, CP 8888, Succ. Centre-Ville, Montréal, Québec, Canada, H3C 3P8
GEOTOP – Geochemistry and Geodynamics Research Center, CP 8888, Succ. Centre-Ville, Montréal, Québec, Canada, H3C 3P8
Department of Geography, Université du Québec à Montréal, CP 8888, Succ. Centre-Ville, Montréal, Québec, Canada, H3C 3P8

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Abstract
Testate amoebae are common proxy for water table depth in peatlands and are commonly used to reconstruct past hydroclimatic conditions. In northeastern America, previous transfer function development was mostly limited to ombrotrophic peatlands from continental and/or oceanic contexts. This study provides a greater range of modern analogues ($n = 206$) from ombrotrophic to poor minerotrophic peatlands along an ecoclimatic gradient from boreal to subarctic in both continental and oceanic regions. Multivariate analysis confirmed that water table depth is the dominant control on species distribution, and a new transfer function was developed for this environmental parameter. The WA.inv model has a RMSEP of 5.44 cm and $R^2$ of 0.80. The effect of spatial autocorrelation on the predictive power and statistical significance of this transfer function was also tested using newly developed statistical tests. We also improved modern analogues for two problematic species (Hyalophenia subflava and Diffugia pulex). This new testate amoeba transfer function will improve paleohydrological reconstructions from high-latitude peatlands (e.g. subarctic fens) and increase our ability to evaluate their sensitivity to ongoing climate change.

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1. Introduction

Over recent decades, testate amoebae (single-celled protists) have become an important paleoecological and paleohydrological indicator in peatlands. These organisms, which thrive in the upper peat layers, are among the most sensitive proxies for water table depth (WTD) (Booth, 2008; Mitchell et al., 2008) and have been widely used in paleohydroclimatic reconstructions from peat records in Europe (e.g. Charman et al., 2006; Langdon et al., 2012). Testate amoebae transfer function development has been mostly restricted to ombrotrophic peatlands in temperate and oceanic regions of the Canadian Atlantic provinces and Eastern United States (Warner and Charman, 1994; Charman and Warner, 1997; Hughes et al., 2006; Booth, 2008; Elliott et al., 2011). Regional comparisons suggest that most taxa have similar positions along the hydrological gradient (e.g. Amphitrema wrightianum, Trigonopyxis arcula type), while some others with poor modern analogues (e.g. Hyalosphenia subflava, Diffugia pulex) tend to vary significantly between regions (Mitchell et al., 2008).

In Canada, ombrotrophic peatlands are widespread throughout the boreal biome, and are gradually replaced by poor minerotrophic systems (fens) northward as peat accumulation is impeded by shorter growing seasons and the influence of permafrost (Payette, 2001). Testate amoebae have been increasingly used as proxies of paleohydrological conditions within the boreal and subarctic peatlands of northeastern Canada (Loisel and Garneau, 2010; van Bellen et al., 2011; Bunbury et al., 2012; Lamarre et al., 2012). The paleoecological interpretations of testate amoeba records are often limited within these ecosystems by the lack of modern analogues covering this biogeographic context. More knowledge is required on the ecology of taxa typical of minerotrophic conditions (fens) to...
support the spatial (climatic gradient) and temporal (fen to bog transition) ecological interpretations. Although the environmental control on testate amoeba communities in fens remains poorly understood, Payne (2011) showed that they can also be used to quantify substrate-moisture in peatlands. However, these results must be taken with caution as this study covered a large variety of trophic conditions from rich minerotrophic peatlands to reed swamps and even drained fens. In the present study, we developed the first testate amoeba-based transfer function that includes modern training sets from boreal and subarctic regions from both minerotrophic and ombrotrophic peatlands. This study aims to (1) evaluate the relationship between testate amoebae and environmental variables; (2) build a new transfer function to improve the paleohydrological reconstructions in high-latitude peatlands; (3) evaluate the differences in terms of species optimism from northern regions to other published testate amoeba studies; and (4) improve knowledge on taxa with poor modern analogues such as H. subflava and D. pulex (Mitchell et al., 2008).

2. Methods

2.1. Regional setting

A total of 18 peatlands have been selected for testate amoeba modern analogue sampling (Fig. 1; Table 1). The sites are located across Québec and belong to the boreal and subarctic bioclimatic regions. They are distributed along south–north (from 45°57′ to 55°13′ N) and west–east gradients (from 78°12′ to 63°32′W) to cover a broad range of peatland types developed within continental to oceanic climate conditions.

<table>
<thead>
<tr>
<th>Location</th>
<th>Code</th>
<th>Latitude (°N)</th>
<th>Longitude (°W)</th>
<th>Peatland type</th>
<th>n sites</th>
<th>WTD range (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kuujjuaapik</td>
<td>KUJU</td>
<td>55°13′32.1</td>
<td>77°41′44.4</td>
<td>Fen</td>
<td>10</td>
<td>3–19</td>
</tr>
<tr>
<td>La Grande</td>
<td>LG2 Fen</td>
<td>53°40′38.3</td>
<td>78°12′58.0</td>
<td>Fen</td>
<td>10</td>
<td>2–23</td>
</tr>
<tr>
<td>La Grande</td>
<td>LG2 Bog</td>
<td>53°39′01.1</td>
<td>77°43′32.3</td>
<td>Bog</td>
<td>10</td>
<td>0.1–28</td>
</tr>
<tr>
<td>Matagami</td>
<td>MTG Bog2</td>
<td>49°41′06.5</td>
<td>77°43′54.3</td>
<td>Bog</td>
<td>10</td>
<td>7.5–47</td>
</tr>
<tr>
<td>Matagami</td>
<td>MTG Bog1</td>
<td>49°45′05.6</td>
<td>77°39′24.5</td>
<td>Bog</td>
<td>6</td>
<td>13–51</td>
</tr>
<tr>
<td>Verendrye</td>
<td>VER</td>
<td>47°18′09.2</td>
<td>76°51′16.4</td>
<td>Fen</td>
<td>4</td>
<td>1–19</td>
</tr>
<tr>
<td>Val-d’Or</td>
<td>VLD</td>
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<td>77°35′43.7</td>
<td>Bog</td>
<td>10</td>
<td>9–44</td>
</tr>
<tr>
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<td>MORTS</td>
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<td>63°40′08.7</td>
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<td>17</td>
<td>1–39.5</td>
</tr>
<tr>
<td>Baie</td>
<td>BAIE</td>
<td>49°05′47.4</td>
<td>68°14′37.6</td>
<td>Bog</td>
<td>7</td>
<td>0.5–28</td>
</tr>
<tr>
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<td>PYL</td>
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<td>73°19′38.4</td>
<td>Fen</td>
<td>3</td>
<td>0.1–14.5</td>
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<tr>
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<td>ABE</td>
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<td>72°30′03.2</td>
<td>Fen</td>
<td>6</td>
<td>0.1–4.5</td>
</tr>
<tr>
<td>Frontenac</td>
<td>FRONT</td>
<td>45°57′59.3</td>
<td>71°08′21.8</td>
<td>Fen</td>
<td>10</td>
<td>0.1–21.5</td>
</tr>
<tr>
<td>Manic</td>
<td>MANIC</td>
<td>49°07′17.9</td>
<td>68°18′02.5</td>
<td>Bog</td>
<td>25</td>
<td>0–43</td>
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<tr>
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<td>LEBEL</td>
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<td>68°14′23.5</td>
<td>Bog</td>
<td>10</td>
<td>–3–38</td>
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<tr>
<td>Lebel</td>
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<td>10</td>
<td>5.5–41.5</td>
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<td>11</td>
<td>0–34</td>
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<td>PLAIN</td>
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<td>63°32′28.5</td>
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<td>15</td>
<td>–6–57</td>
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<tr>
<td>Roma</td>
<td>ROMA</td>
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<td>63°41′35.1</td>
<td>Bog</td>
<td>25</td>
<td>1–40</td>
</tr>
</tbody>
</table>

Fig. 1. Location of the study sites in Québec. Details for each site are listed in Table 1.

2.2. Modern training set collection and laboratory analyses

A total of 206 modern surface peat samples were collected and treated for transfer function modelling following the ACCROTEL protocol (http://www2.glos.ac.uk/accrotem/fieldst.html). In order to minimize the statistical bias associated with the clustered design of modern training sets (Payne et al., 2011), we sampled a large number of sites (n = 18), integrated a wide diversity of peatlands (poor fen to domed bog) over significant latitudinal gradients, and covered the full microtopographic gradient (from high and low hummocks to pool margins; no high hummocks in fens). Surface peat samples (10 × 10 × 10 cm) were cut with a serrated knife before being placed in sealed plastic bags. Peat temperature (upper 5–10 cm) was measured using a VWR 23609-234 digital thermometer equipped with a 10-cm probe rod. Surface moisture was evaluated with a HH2 Moisture Meter (Delta-T devices) from the oceanic sites only (Saint-Lawrence North Shore; n = 90). Water table depth was measured relative to the surface in the cavity left by the sampling after at least 30 min (Payne et al., 2006) while pH was obtained from interstitial water of surface peat. In the laboratory, each peat sample was cut in half, electric conductivity was measured from the squeezed water of one half of the sample and the other half was treated for testate amoeba analysis. Due to the vertical distribution of testate amoeba communities (Mitchell and Gilbert, 2004), only the upper 3–5 cm of the Sphagnum stems under the capitulum was treated (Payne et al., 2006; Booth, 2008). Tests were extracted following a standard protocol (Hendon and Charman, 1997; Charman et al., 2000). Peat subsamples were gently boiled in distilled water for 10 min and wet-sieved through 355 and 15 µm mesh screens. The remaining portion was then mixed with glycercinated water (30%) in 15 ml tubes and centrifuged at 3000 rpm for 10 min. Residual material was stained and mounted on glass slides and analyzed at a 400× magnification with an optical microscope. A minimal count of 100 individuals was achieved, as suggested by Payne and Mitchell (2009). Species identification was based on test morphology detailed in Charman et al. (2000). Along with testate amoebae, rotifer shells of Habrotricha angusticollis were also counted, but were not included in the transfer function database.

2.3. Multivariate analysis

Ordination analyses were conducted with PC-ORD 6 software (McCune and Mefford, 2011). Species–environment relationships were explored using canonical correspondence analysis (CCA), a technique which performs well with unusual sampling design and highly correlated environmental variables (Palmer, 1993). CCA
analyses were conducted on a reduced dataset of 181 samples for which water table depth, conductivity, pH and peat temperature were available. Taxa with less than three occurrences were excluded from the CCA ordinations. Further partial CCAs were conducted on each environmental variable to estimate the variance partitioning. A Monte Carlo permutation test was used to determine the statistical significance of the species–environment relationships.

2.4. Transfer function development

A total of 64 different testate amoeba taxa were identified from the surface samples but those with less than five occurrences and that never reached 5% in abundance were removed from the dataset, leaving a total of 47 taxa. Transfer functions were built using the Rioja (Juggins, 2012) and palaeoSig (Telford, 2011) packages available in R CRAN (R core Team). As it was previously shown that Weighted average (WA) based models are the most robust for spatial autocorrelation (Telford and Birks, 2005; Amesbury et al., 2012), we developed four WA models (WA.inv, WA.cla, WA.inv.tol, WA.cla.tol). Their performances were evaluated using bootstrap cross-validation (1000 cycles). These models were optimized by removing samples with high residual values (20% of the entire WTD range), based on the screening of the predicted versus observed values (Charman et al., 2007; Payne and Mitchell, 2007). Additionally, samples with score values superior to two (2) on the secondary axis of the CCA analyses (Fig. 3) were removed from the transfer function, as we assumed that these samples were primarily influenced by pH. The evaluation of model performances was based on $R^2$, root mean square error of prediction (RMSEP) and maximum bias (MaxBias). Tests for the influence of spatial autocorrelation on the transfer functions were also conducted, as suggested by Telford and Birks (2009) and Amesbury et al. (2012). To test its applicability to reconstruct past WTD, we applied our transfer function to the fossil testate amoeba record of Lac Le Caron peatland from the James Bay region. We finally compared our WTD reconstruction to those performed by Amesbury et al. (2012) and Booth (2008). Finally, in order to show that our transfer model is statistically significant, our reconstruction was compared to 999 simulations trained on randomly generated WTD (Telford and Birks, 2011b).

![Fig. 2. Canonical Correspondence Analysis (CCA) of the reduced dataset of 181 modern samples showing the species–environment relationship.](image-url)
3. Results

3.1. Canonical correspondence analysis (CCA)

Constrained ordination with CCA shows that the main axis of species variation (axis 1) is strongly correlated to water table depth \( (r = -0.85, p < 0.001) \) (Fig. 2). The Monte Carlo permutation test showed that axis 1 is highly significant \( (p < 0.001, 999 \text{ random permutations}) \). CCA axis 2 is mainly correlated to \( \text{pH} \) \( (r = -0.67, p < 0.001) \). Axis 1 and 2 explain 11.7% of the variability in the contemporary testate amoeba dataset and 71% of the species–environment relationship. Partial CCAs show that WTD and \( \text{pH} \) are both significant \( (p < 0.001) \) and explain respectively 7.6% and 4.2% of the species variability. Further CCAs of the subgroup of modern samples from the maritime region (Saint-Lawrence North Shore) \( (n = 90) \) shows that surface moisture is also strongly correlated to axis 1 \( (r = 0.86) \) and explains 8.7% of the variability in these assemblages.

The constrained ordination of the samples with CCA shows some overlap in the assemblages from different sites but distinct pattern between bog and fen samples (Fig. 3). The bog assemblages are preferentially controlled by the hydrological gradient (axis 1) whereas the fen assemblages are more influenced by \( \text{pH} \) along axis 2. Further CCAs performed separately on the fen and bog subsets \( (n = 45 \text{ and } n = 136 \text{ respectively}) \) show that although \( \text{pH} \) explains more species variability in fens (5.8%), WTD remains the most important controlling variable in these samples (variance explained = 9.5%).

3.2. Transfer function development

The multivariate analysis shows that modern testate amoeba communities are significantly correlated to water table depth and confirms that a transfer function can be developed for this variable. Overall, the optimized WA models show good performance statistics for \( R^2 \) and RMSEP (Fig. 4, Table 2). Although each WA model could be used in theory, the capacity of the WA-inv to predict WTD on LLC was optimal, we have thus retained this model for further statistical testing (Fig. 5).

Additional cross-validation tests were conducted to estimate the influence of spatial autocorrelation within the dataset (Telford and Birks, 2009). Fig. 6 presents \( R^2 \) decreases associated with the removal of geographical neighbors (0, 1, 50, 250, 500 km) compared to the removal of randomly-selected sites (0–90% sites deleted at random). The \( R^2 \) drops from 0.80 to 0.74 both with the removal of geographical neighbors and the random deletion of sites. Differences between the two \( R^2 \) drops are systematically inferior to 5% for the full geographical gradient. This suggests that spatial autocorrelation in not an issue in our dataset, an aspect that reinforces the validity of the performance statistics.

3.3. Evaluating the transfer function on a fossil sequence

We have tested the statistical validity of our transfer function to reconstruct past WTD on Lac le Caron (LLC) record by comparing our reconstructions from our models to the one inferred from to 999 transfer functions based on randomly generated WTD data (Telford and Birks, 2011b) (Fig. 5). The statistical significance of the transfer function model is confirmed by that procedure as weighted correlations between species optima and the first ordination axis scores are higher or very close to 95% of the reconstructions generated from random WTD data (Fig. 5).

We applied the new WA-inv model on Lac Le Caron record (James Bay lowlands) and compared the inferred WTD with those produced with the modern datasets of Booth (2008) (van Bellen et al., 2011) and Amesbury et al. (2012) (Table 3). Our WA-inv reconstruction is very similar to the one of Booth (2008): the only difference is that our model produced lower WTD values in some sections (Fig. 7). The reconstruction from Amesbury et al. (2012) shows the same overall tendencies but with much lower amplitude of variations.

### Table 2

<table>
<thead>
<tr>
<th>Models</th>
<th>Number of samples</th>
<th>( R^2 )</th>
<th>Max bias</th>
<th>RMSEP</th>
</tr>
</thead>
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<td>WA.inv</td>
<td>199 (165)</td>
<td>0.63 (0.80)</td>
<td>24.49 (9.40)</td>
<td>7.39 (5.44)</td>
</tr>
<tr>
<td>WA.cla</td>
<td>199 (165)</td>
<td>0.63 (0.80)</td>
<td>19.24 (5.75)</td>
<td>8.39 (5.80)</td>
</tr>
<tr>
<td>WA.inv.tol</td>
<td>199 (165)</td>
<td>0.67 (0.81)</td>
<td>25.98 (9.20)</td>
<td>7.48 (5.34)</td>
</tr>
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<td>WA.cla.tol</td>
<td>199 (165)</td>
<td>0.67 (0.82)</td>
<td>22.40 (5.98)</td>
<td>8.27 (5.65)</td>
</tr>
</tbody>
</table>

4. Discussion

4.1. Species–environment relationship

The constrained ordination using CCA corroborates the results of previous studies showing that hydrological variables (WTD and moisture) are the strongest environmental control on the
distribution of testate amoebae (e.g. Payne et al., 2006; Charman et al., 2007; Payne and Mitchell, 2007; Booth, 2008; Lamentowicz et al., 2008; Swindles et al., 2009; Amesbury et al., 2012). In the minerotrophic samples, water table depth was also the most important environmental factor, but the CCA ordination (Fig. 3) suggests that pH has a greater influence on the testate amoeba communities within these environments. Although no taxa were exclusive to fens, the distribution of some species such as Centropyxis platystoma type, Nebela tubulosa type, Quadrulella symetrica and Sphenoderia lenta seems clearly related to a nutrient status associated with pH (Fig. 2). These results globally support those of Payne et al. (2011), who found that testate amoebae are sensitive surface-moisture proxies in poor minerotrophic environments as well. However, our results may not be extended to nutrient-rich environments since most of our minerotrophic sites had a poor nutrient status (poor fens). Testate amoeba communities are sensitive to water table in fens, but transfer functions developed for these systems may result in models with lower predictive performance considering the importance of environmental factors related to water chemistry (e.g. pH). Hence, more sampling efforts are clearly needed from different types of minerotrophic peatlands to fully explore the species ecology within these environments. However, considering the small gradients of water table depths in minerotrophic environments, the inclusion of their samples could amplify clustering effect and spatial autocorrelation within the dataset and make it impossible to build statistically valid transfer functions.

There remains a high percentage of unexplained variance in the modern testate amoeba dataset, which is partially explained by inter-correlations between variables or unmeasured environmental factors. As shown by Sullivan and Booth (2011), testate amoebae distribution in peatlands is also influenced by short-term environmental variability, a factor which may be particularly important in boreal and subarctic peatlands influenced by considerable seasonal hydroclimatic variations. Although vegetation types do not implicitly control testate amoeba distribution (Woodland et al.,

![Fig. 4. Observed versus estimated water table depth values from the WA.inv model. Left: on the complete dataset and Right: after the screening of samples with high residual values and taxa with low occurrences.](image)

![Fig. 5. Histograms showing the weighted correlation between species optima and the first ordination axis scores for each WA model tested with the LLC dataset. Grey histograms represent the distribution of the correlations obtained from 999 reconstructions calibrated on randomly generated WTD. The dashed line represents the 95th percentile of the distribution. The solid line represents the value of the correlation when the observed WTD values are used.](image)
the short-term environmental variability seems to be buffered by vegetation structure and density (Sullivan and Booth, 2011) and may also differ between microforms, peatland types (bogs and fens) and latitude. In northern peatlands, seasonal freezing or permafrost within the subsurface peat generates drier conditions which in turn impact on thermal conductivity and influence its duration. Hence, seasonal freezing or permafrost may significantly increase the subsurface environmental variability (from dry when frozen to wet when melting) and this factor needs to be further investigated in nordic systems.

4.2. A new transfer function for water table depth reconstructions adapted to high-latitude peatlands

Our transfer function models show very good performance statistics to predict water table depth. The RMSEP is similar to those obtained by Amesbury et al. (2012). Our results also show that spatial autocorrelation has a very limited impact on the predictive power of the WA model (Fig. 6) and that our paleohydrological reconstruction is statistically significant (Fig. 5). Therefore, the statistical techniques developed by Telford and Birks (2009, 2011a) have greatly helped in evaluating the robustness of our transfer

![Fig. 6. Plot showing effect of spatial autocorrelation on $R^2$ after the removal of randomly selected sites (open circles) and sites in the geographical neighbourhood of the test site (filled circles).](image)

Fig. 6. Plot showing effect of spatial autocorrelation on $R^2$ after the removal of randomly selected sites (open circles) and sites in the geographical neighbourhood of the test site (filled circles).

![Fig. 7. Comparison of the different water table depth (WTD) reconstructions on the fossil testate amoebae record of Lac Le Caron (van Bellen et al., 2011).](image)

Fig. 7. Comparison of the different water table depth (WTD) reconstructions on the fossil testate amoebae record of Lac Le Caron (van Bellen et al., 2011).
Fig. 8. Water table depth (WTD) optima and tolerances of the 47 remaining taxa of our WA.inv model.
function while choosing most appropriate WA.inv model to reconstruct long-term WTD variability at LLC.

4.3. Testing the transfer function models on a fossil record

The WTD reconstruction produced by our WA.inv model on the fossil record of Lac Le Caron peatland (van Bellen et al., 2011) was very similar to the one based on Booth (2008) (Fig. 7). However, there were clear discrepancies with Amesbury et al. (2012) that show much lower amplitude of WTD variations. This difference is mainly explained by the poor modern analogue for some taxa such as *D. pulex*, as underlined by Amesbury et al. (2012). Their results suggest that this species has a relatively wet optima which differs significantly from our study and other published transfer functions showing intermediate (Charman et al., 2007; Booth, 2008) and even very dry WTD optima (Turner et al., 2013) for *D. pulex* (Fig. 8). These differences may arise from poor modern analogues or potential identification confusion that may result in difficulties in inferring proper range of species WTD optima and tolerances. Considering that Lac Le Caron peat record, as in many other Holocene peat sequences, contains significant abundances of *D. pulex* (van Bellen et al., 2011), it was crucial to improve modern analogues for this species.

4.4. Improving modern analogues from boreal and subarctic regions

In the present study, most testate amoeba species occupy similar positions along the water table depth gradient compared to previously published transfer functions (Booth, 2008; Amesbury et al., 2012; Turner et al., 2013) (Fig. 8). This suggests that the testate amoeba response to water table depth does not vary significantly between the bioclimatic contexts. Species such as *Difflugia globulosa* type and *A. wrightianum* have very wet optima in different peatland types of all regions while *T. arcula* type and *Bullinularia indica* are confirmed as reliable indicators of very dry conditions. We have improved modern analogues for *D. pulex* (44 occurrences) and *H. subflava* (51 occurrences) although their abundance was relatively low in most samples. *D. pulex* has a dry to intermediate WTD optima (20.9 cm), whereas *H. subflava* is confirmed as a dry indicator (WTD optima = 24.5 cm). However, both species seem to have a complex distribution along the water-table gradient as they were found in wet fen environments as well as dry bog hummocks. Sullivan and Booth (2011) have suggested that these two taxa are characteristics of sites with highly variable environmental conditions. Additional research is required to increase our knowledge on the response of testate amoeba communities to seasonal variations. Little is known about the impact of seasonal freezing and permafrost on testate amoeba communities particularly on their relation with active layer thickness and surface-wetness during the summer. Other environmental factors also need to be further considered in northern conditions such as wind exposure which increases peat surface desiccation without directly affecting the water table depth. Improving the understanding of species response to environmental stress like permafrost, seasonal frost and wind-exposure will eventually improve palaeoecological interpretations for some species like *D. pulex* and *H. subflava* which are dominant in fossil assemblages but poorly represented in modern analogues.

5. Conclusion

We developed and tested a new paleohydrological tool adapted to both *Sphagnum*-dominated bogs and poor fens from boreal and subarctic environments. The results of our study supplied a greater range of analogues over a wide geographic and ecoclimatic gradient in northeastern Canada. Hence, this new testate amoeba transfer function provides a reference for further climate reconstruction from northern environments. As northern peatland ecosystems are undergoing significant transformations (Payette et al., 2004; Turetsky et al., 2007; Vallée and Payette, 2007), the development of adapted paleohydrological tools will improve our ability to evaluate their sensitivity. In the future, particular attention should be given to the ecology of testate amoebae in sites experiencing a wide range of moisture variability particularly in subarctic environments where frost dynamics play an important role in peatland hydrology. Further data from such environments will greatly improve the comprehension of hydrological variations on these ecosystems and their impact on the carbon dynamics. Considering the lack of modern analogues from northern peatlands, this transfer function is the first step towards the development of a fully adapted and functional tool to infer paleohydrological conditions in these environments.

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References


