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Short communication

Significance testing testate amoeba water table reconstructions

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ABSTRACT

Transfer functions are valuable tools in palaeoecology, but their output may not always be meaningful. A recently-developed statistical test ('randomTF') offers the potential to distinguish among reconstructions which are more likely to be useful, and those less so. We applied this test to a large number of reconstructions of peatland water table depth based on testate amoebae. Contrary to our expectations, a substantial majority (25 of 30) of these reconstructions gave non-significant results ($P > 0.05$). The underlying reasons for this outcome are unclear. We found no significant correlation between randomTF P-value and transfer function performance, the properties of the training set and reconstruction, or measures of transfer function fit. These results give cause for concern but we believe it would be extremely premature to discount the results of non-significant reconstructions. We stress the need for more critical assessment of transfer function output, replication of results and ecologically-informed interpretation of palaeoecological data.

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1. Introduction

Testate amoebae are widely-used proxies in palaeoecological

studies; in particular for the reconstruction of water table depth in peatlands (Charman, 2001; Mitchell et al., 2008). Over the last 25 years palaeoecology has been revolutionised by the use of statistical models (transfer functions) to quantitatively reconstruct environmental variables. However, questions are increasingly being raised about the reliability and robustness of transfer function results (Belyea, 2007; Juggins, 2013).

A transfer function will always give an output but that output

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may not always be meaningful. The only way to establish whether the output of a transfer function is 'true' is by comparing the results to independent data, but such data are not always available and even in such cases correlations are complicated by temporal autocorrelation and the limitations of the chronology.

Although we cannot realistically assess whether all reconstructions are correct we can conceivably test whether they are potentially useful. Telford and Birks (2011) propose a pragmatic solution: that a reconstruction can be considered statistically significant if it explains more of the variance in the fossil data than those of transfer functions trained on randomly-generated data. Telford and Birks (2011) propose a method, 'randomTF', in which:

1. The transfer function is applied to the fossil data to derive a reconstruction (using any commonly-applied method).
2. The proportion of variance in the fossil data explained by the reconstruction is determined using constrained ordination.
3. Multiple new transfer functions are derived using the established modern species data but with the environmental data replaced by uniformly distributed random variables.
4. These transfer functions are applied in turn to the fossil data and the variance they explain tested. This is repeated a large number of times, typically 999.
5. A reconstruction is considered statistically significant when the proportion of variance explained is greater than that of 95% of the transfer functions based on randomly-generated data.

We would expect reliable reconstructions to explain more variance in the fossil data than transfer functions trained on random data, and therefore to give significant results. However, a significant randomTF value is not proof of accuracy and a non-significant result does not necessarily imply inaccuracy. Non-significant results do however give cause for concern and suggest that transfer function output should be treated with caution. randomTF tests can potentially tell us which reconstructions we should trust more, which less, and whether we can predict more than one environmental variable from the same fossil dataset. Telford and Birks (2011) also propose an alternative test ('obs.cor') based on the correlation of optima values with axis species scores from a constrained ordination of the fossil data. This test is not applicable to all transfer functions methods and is not considered here. The randomTF test has been applied in a few studies (Amesbury et al., 2013; Lamarre et al., 2013; Swindles et al., 2015a) but is not yet routinely used in testate amoeba palaeoecology. Here we apply this test to a large number of published and unpublished records with the aim to identify the characteristics which are likely to lead to better reconstructions, giving better randomTF results.

2. Methods

We identified 30 published and unpublished testate amoeba palaeoecological records (Table 1). These records span a large range of regions, mire types, analysts, time periods, and sampling resolutions, and form a large and reasonably representative sample of testate amoeba palaeoecological research. Reconstructions of water table depth were produced using either the transfer function used in the original study, the most geographically-appropriate model where a transfer function was not previously applied, or in a few cases transfer functions which have been produced since the data were originally published. Taxonomy was harmonised between the fossil data and training set, which in many instances required the grouping or deletion of some taxa (performance statistics may therefore differ slightly from those previously published). Transfer functions were applied based on the model selected by the original authors with sample specific errors calculated by bootstrapping

(1000 cycles). All transfer functions were based on either weighted averaging, weighted averaging with tolerance downweighting or weighted average-partial least squares (Birks, 1995). We applied randomTF using 999 permutations with redundancy analysis as the ordination method. Analyses were conducted in R3.1.2 (R Development Core Team, 2014) using the packages analogue (Simpson, 2007), rioja (Juggins, 2009) and palaeoSig (Telford, 2011).

3. Results and discussion

Only five of the 30 tests yielded a significant P-value ($P < 0.05$; Table 1). While we expected that some reconstructions would give non-significant results this proportion is much higher than we anticipated. While a few reconstructions fail to reach $P = 0.05$ by a relatively narrow margin (Tørvesø 1, Staroselsky Moch, Dot Lake B), many more have P-values which substantially exceed this value.

Another two records published in the literature have given significant P-values: those of Swindles et al. (2015a) for Stordalen, Sweden and Lamarre et al. (2013) for Lac Le Caron, Canada. Amesbury et al. (2013) found a significant result for the Nordans Pond site of Hughes et al. (2006) using an extended transfer function, whereas here we find a non-significant result using the transfer function used in the original study (Charman and Warner, 1997). In the latter three cases multiple model structures were tested with some producing significant reconstructions, and some not. We note that in these instances a correction for multiple comparisons (such as a Bonferroni correction) would probably have meant that the reconstructions did not reach significance. However, even if these results are included, eight significant P-values out of 32 reconstructions remains a surprisingly low proportion.

Telford and Birks (2011) identify four factors which might make the randomTF test prone to type II error ("false negative"): low numbers of effective species; small numbers of fossil samples; limited variability in the reconstruction and poorly-performing or poorly-fitting transfer functions. All of these factors apply to some of the reconstructions we examine but it is not clear that any are a consistent cause of non-significant P-values. Overall, P-value was not significantly correlated with properties of the training set (mean, standard deviation or range of WTD) or fossil data (species richness, Hill's N2 or number of samples), performance metrics of the transfer function (leave one out RMSEP or R^2), properties of the reconstruction (mean, standard deviation or range of predications, ratio of prediction range to RMSEP or training set range, mean bootstrapped error estimates) or measures of transfer function fit (proportion of shared taxa, proportion of fossil samples with poor modern analogues, squared residual length) (Spearman R_s ; $P > 0.05$). P-value was strongly correlated with the proportion of variance in the fossil data explained by the reconstruction (Spearman $R_s = -0.89$, $P < 0.001$), suggesting (unsurprisingly) that where a high proportion of variance is explained this is unlikely to be exceeded by transfer functions trained on random data.

The five reconstructions yielding significant results were three short records from the Elatia Forest of northern Greece (Dexameni; Krya Vrissi 1&2; Payne and Pates (2009)), the high-resolution Mauntschas record from the Swiss Alps (Lamentowicz et al., 2010; van der Knaap et al., 2011) and a record from Frasné in the Jura Mountains of eastern France (Jassey et al. unpublished). These five records have little obvious similarity. The transfer functions used for the Dexameni, Krya Vrissi and Mauntschas reconstructions all included samples from the same sites and for Frasné the closest training set site was only c.10 km distant. However, ten of the sites with non-significant reconstructions were also included in their respective training sets. The three short records from Greece (Payne and Pates, 2009) are all characterised by a single large change—a shift to drier conditions in the recent past but this is not a feature of

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