An alternative approach to transfer functions? Testing the performance of a functional trait-based model for testate amoebae

CrossMark

Simon van Bellen [a,*], Dmitri Mauquoy [a], Richard J. Payne [b], Thomas P. Roland [c,1], Paul D.M. Hughes [c], Tim J. Daley [d], Neil J. Loader [e], F. Alayne Street-Perrott [e], Emma M. Rice [f], Verónica A. Pancotto [g]

[a] School of Geosciences, University of Aberdeen, UK
[b] Environment Department, University of York, UK
[c] Geography and Environment, University of Southampton, UK
[d] Sustainable Earth Institute, University of Plymouth, UK
[e] Department of Geography, College of Science, Swansea University, UK
[f] School of Geography, University of Plymouth, UK
[g] CADIC/CONICET, Argentina

ARTICLE INFO

ABSTRACT

Transfer functions are now widely available to infer past environmental conditions from biotic assemblages. Existing transfer functions are based on species assemblages but an alternative is to characterize assemblages based on functional traits, characteristics of the organism which determine its fitness and performance. Here, we test the potential of trait-based transfer functions using testate amoeba functional traits to reconstruct peatland water-table depths.

A total of seven functional traits with linkages to peat moisture content were identified and quantified as community weighted-means for each of 43 taxa in a training set from Tierra del Fuego, South America. Transfer functions based on (multiple) linear regression and partial least-squares were produced, validated using cross-validation and an independent test set, and applied to three core records. Trait-based models performed remarkably well. Model performance based on cross-validation and an independent test set was only marginally weaker than for models based on species and reconstructed down-core trends were extremely similar. Trait-based models offer considerable potential for paleoecological reconstruction particularly in no-analogue situations, where no species transfer function is available and for inexperienced analysts. The approach deserves further validation and testing for both testate amoebae and other groups of microfossils.

© 2016 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

Transfer functions are frequently applied to biostratigraphic indicators from sediments to quantify past changes in environmental variables. Frequently used combinations of indicators and predicted variables include pollen-temperature/precipitation (Klemm et al., 2013), chironomids-temperature (Massaferro and Larocque-Tobler, 2013), foraminifera-sea level (Kemp et al., 2013) and testate amoebae-water water-table level (Amesbury et al., 2016; Lamarre et al., 2013). These transfer functions are based on the principle of uniformitarianism and assume that there is a direct relationship between the environmental variable to be reconstructed and the abundance of individual taxa and that the relationship has remained constant through time (Birks et al., 2010). All published transfer functions have in common that the biotic assemblages are defined by their taxonomy, e.g. to family, genus or species level. However, a possible alternative may be considered, which is to base transfer functions on functional traits. Functional traits are the key characteristics of an organism which determine its fitness or performance (Green et al., 2008). Species with similar traits are likely to perform similar roles in the ecosystem and favour similar environmental conditions. Defining an assemblage based on functional traits has the advantage of providing a mechanistic link with ecosystem processes and environmental conditions which may therefore give more information on ecosystem functioning than taxonomy alone (Barnett et al., 2007; Tilman et al., 1997). The use of functional traits has attracted increasing interest in paleoecology primarily with the aim to better understand the mechanisms underlying past assemblage change (Eronen et al., 2010; Lacourse, 2009; Marcisz et al., 2016). However, the possibility of building transfer functions based on traits rather than species has not been previously explored. Trait-

* Corresponding author at: GEOTOP-Université du Québec à Montréal, CP 8888, Succ. Centre-Ville, Montréal, H3C 3P8, Canada.
E-mail address: van_bellen.simon@uqam.ca (S. van Bellen).
[1] Now at Geography, College of Life and Environmental Sciences, University of Exeter, UK.

based transfer functions may have three possible advantages: 1) they may offer superior performance if the functional trait assemblage of a sample is more strongly linked to an environmental variable than the species assemblage; 2) they may be more generalizable, allowing a transfer function to be applied to species not included in the training set based on functional traits which are included, and 3) they may be more robust to problems of taxonomic resolution and error, as traits may often be easier to determine than species. Here, we evaluated and compared the performance of transfer functions based on species and trait assemblages, using testate amoebae and peatland water-table reconstructions as a case study.

Testate amoebae are a polyphyletic collection of at least three taxonomic groups of unicellular eukaryotes (Kosakyan et al., 2016a). The shells (tests) of these organisms have been studied as indicators of ecosystem health (Fournier et al., 2012), sea level change in marshes (Charman et al., 2010) and lake water quality (Neville et al., 2013; Roe et al., 2010), but most frequently to reconstruct past water-table dynamics in mid- and high-latitude, mostly ombrotrophic, peatlands (e.g. Mitchell et al., 2001; Warner and Charman, 1994). Such reconstructions may reflect past changes in hydroclimate (e.g. Booth, 2002; Charman et al., 1999; Lamentowicz et al., 2010) and may be linked to past variability in carbon sequestration rates at decadal to millennial timescales (Charman et al., 2015; Loisel and Garneau, 2010; van Bellen et al., 2011). Compared with other indicators frequently analyzed in peatlands, such as plant macrofossils, testate amoebae respond quickly to environmental change because of their short life span and high rates of reproduction (in the order of 10–27 generations per year; Charman, 2001). Transfer functions have been developed for several regions around the globe (Amesbury et al., 2013; Booth, 2008; Charman et al., 2007; Lamarre et al., 2013; Payne et al., 2008; Qin et al., 2013; van Bellen et al., 2014), motivated by regional differences in peatland ecohydrology and taxa distribution and associated ecological preferences.

Lack of consistency in the current taxonomy is considered a major issue which may affect the quality of the reconstructions from testate amoeba assemblages (Heger et al., 2009; Kosakyan et al., 2016a; Payne et al., 2011). Testate amoeba taxonomy is based largely upon 'morphospecies', i.e. defined by test morphology, and phylogenetic data remains sparse, despite recent efforts (e.g. Gomaa et al., 2013; Kosakyan et al., 2016b; Lahr et al., 2011). Testate amoeba studies frequently group cryptic species, which cannot be identified solely by morphology (e.g. the genus *Nebela*; Oliverio et al., 2014), and pseudo-cryptic species, which have only very subtle morphological dissimilarities (Singer et al., 2015). A range of identification keys for testate amoeba identification and quantification have been developed (e.g. http://istar.wikidot.com/id-keys and Charman et al., 2000) but include many inconsistencies. While this may be due to the parallel development of original taxonomies, the potential for real geographical differences in shell morphology cannot be excluded. Rare taxa with low abundance or with presence restricted to a few samples, are often excluded from the assemblage prior to the application of a species-based transfer function, because their optimal water-table depth may be uncertain. The elimination of taxa represents a loss of information for reconstructions. Low taxonomic resolution and inconsistencies in the identification of testate amoebae may lead to significant biases in quantitative environmental reconstructions (Mitchell et al., 2014; Payne et al., 2011).

Functional traits of testate amoebae have been increasingly considered since a first study by Mitchell and Gilbert (2004). Some important functional traits of testate amoebae can be readily identified and measured based on the morphological characteristics of their test. Functional traits have been investigated primarily to increase the understanding of the interactions between these organisms and their microenvironment (Fournier et al., 2016; Fournier et al., 2015; Jassey et al., 2013b; Lamentowicz et al., 2015; Marcisz et al., 2016) but the use of functional traits in transfer function development has not been addressed. These studies presume functional traits are stable per taxon and taxon

response to variations in environmental conditions is a function of their functional traits. Conversely, the behavioural and morphological characteristics of testate amoebae may provide information on ecosystem characteristics and functioning. Mechanistic relationships between some of these traits and peat surface wetness conditions have now been documented. For instance, a testate amoeba with a small and compressed test is likely advantaged, and thus more abundant, under low moisture conditions, because it will be better adapted to living in a thin water film (Fournier et al., 2012). The relative exposure of the aperture may be an indication of the resistance to drought, with a cryptostomic morphology ('concealed' aperture) being best adapted to such conditions (Fournier et al., 2012; Lamentowicz et al., 2015; Marcisz et al., 2016). Given the possibility that functional traits may vary within the accepted taxonomy, e.g. the number of pores in the test of *Hyalosphenia papilio* (Booth and Meyers, 2010), traits should be selected that are unlikely to show high intra-taxon variability. For instance, testate amoeba biovolume may vary by almost three orders of magnitude between taxa found within the same ecosystem (Fournier et al., 2012), so slight intra-taxon variability is likely to be insignificant compared to the large differences in biovolume among taxa.

The direct links between shell morphology and wetness, combined with the well-known inadequacies of the current morphospecies taxonomy, suggest that there is potential for an alternative approach to paleoenvironmental reconstructions. We hypothesize that better reconstructions may be produced using transfer functions based solely upon traits, which can be objectively determined, rather than using transfer functions based on uncertain and inconsistent morphospecies taxonomy. We therefore developed and tested a testate amoeba transfer function entirely based on functional traits using a previously-published training set sampled in Tierra del Fuego, southernmost South America (van Bellen et al., 2014). Here we compare the performance of trait-based and morphospecies-based transfer functions and apply both down-core to compare inferred water-table depths.

2. Methods

2.1. Fieldwork and laboratory work

The training set used for transfer function construction was the 2012 dataset from van Bellen et al. (2014). This dataset includes a total of 99 samples from four peatlands along with measurements of water-table depth (WTD), pH and electrical conductivity (EC). These peatlands are ombrotrophic with dominance of *Sphagnum magellanicum* from low lawns up to the highest hummocks. Sampling was performed along a total of 20 transects spanning the entire hollow-hummock gradient, which represented a water-table level range of 104 cm. Study region and site characteristics as well as field sampling methods have been described in van Bellen et al. (2014).

2.2. Trait data and community-weighted means

Functional trait values for each taxon, summarized in Table S1, were based on our own unpublished measurements. The functional traits tested included:

1) Test biovolume, believed to be positively related to peat surface wetness, because larger tests need thicker water films to maintain their position within the peat matrix (Laggoun-Défarge et al., 2008). For biovolume calculations, the formulas from Fournier et al. (2015) were used.

2) Aperture position, which is believed to minimize sensitivity to droughts, because more cryptic apertures are less exposed to moisture loss and thus allows for survival in low humidity conditions (Fournier et al., 2012).

3) Test compression, which is considered an adaptation to thin water films and dry conditions (Fournier et al., 2012; Jassey et al., 2013a).