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Palaeoecology of testate amoebae in a tropical peatland

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Abstract

We present the first detailed analysis of subfossil testate amoebae from a tropical peatland. Testate amoebae were analysed from a 4-m peat core from western Amazonia (Peru) and a transfer function developed from the site was applied to reconstruct changes in water table over the past ca. 8,000 years. Testate amoebae were in very low abundance in the core, especially in the lower 125 cm, due to a combination of poor preservation and obscuration by other organic matter. A modified preparation method enabled at least 50 testate amoebae to be counted in each core sample. The most abundant taxa preserved include *Centropyxis aculeata, Hyalosphenia subflava, Phryganella acropodia* and *Trigonopyxis arcula*. *Centropyxis aculeata*, an unambiguous wet indicator, is variably present and indicates several phases of near-surface water table. Our work shows that even degraded, low-abundance assemblages of testate amoebae can provide useful information regarding the long-term ecohydrological developmental history of tropical peatlands.

Keywords: Amazonia; Palaeoecology; Peatlands; Testate amoebae; Tropical rainforest

Introduction

Tropical peatlands represent one of the largest pools of terrestrial organic carbon (C) on Earth and are found in Asia, Africa and South America (Page et al., 2011; Lähteenoja and Page, 2011). The ~89 Pg of C held in tropical peatlands (Page et al., 2011) is similar in amount to that stored in the total aboveground live biomass of the entire Amazon rainforest (93 ± 23 Pg C; Malhi et al., 2006). Despite the importance of tropical peatlands in the global carbon cycle, relatively little is known about the ecohydrological dynamics of these systems and the sensitivity of their carbon stocks to climate change. A greater understanding of long-term hydrological change in tropical peatlands, whether driven by autogenic or allogenic (e.g. climate) factors is needed, as enhanced drought is predicted for many tropical areas in future climate change scenarios.

Testate amoebae are established as important hydrological indicators in mid- and high latitude peatlands (e.g., Charman and Warner, 1992; Tolonen et al., 1994; Charman et al., 2000) as development of transfer functions have enabled quantitative reconstruction of bog palaeohydrology from subfossil tests (Charman et al., 2007; Lamentowicz et al. 2008; Amesbury et al., 2013; Turner et al., 2013; Swindles et al., 2014). Recent research suggests that testate amoebae show distinct responses across hydrological gradients in a tropical peatland in Amazonia and therefore may have potential as palaeohydrological indicators in tropical peatlands (Swindles et al., 2014). However, no detailed studies of subfossil testate amoebae preserved in tropical peats exist at present. In this paper we examine the utility of testate amoebae assemblages preserved in a core collected from the same Amazonian peatland where modern testate amoebae were investigated (Swindles et al., 2014) to evaluate their potential in palaeoecological studies of tropical peatlands.

Material and Methods

Study site

Aucayacu (meaning “water of the natives” or “water of the warriors” in the language of indigenous people) is an ombrotrophic peat dome in Peruvian Amazonia (Lähteenoja et al., 2012). It is situated on alluvial sediments between the Tigre River and a stream of the Pastaza fan (Figure 1). The peatland formed as a nutrient-rich minerotrophic system that gradually developed into an ombrotrophic raised bog (Lähteenoja et al., 2012). Aucayacu represents the deepest and oldest peatland discovered in the Amazon basin (~7.5 m thick in the centre). Peat initiation at the centre of the site is dated to c. 8870 cal. BP (Lähteenoja et al., 2012). The vegetation of Aucayacu is characterised by 'pole' and 'dwarf' forest communities (Figure 2; Swindles et al., 2014). For further information on the vegetation and geochemistry of the site see Swindles et al. (2014). In Iquitos (120 km east of the study site), average annual rainfall of up to 3,000 mm is typical, with a wetter period between the months of November to March (Martinez et al., 2011). The average annual temperature at Iquitos is 26°C, with a diurnal range of approximately 10°C (30-32°C daytime temperatures and 21-22°C at night) (Met Office, 2011).

Methods

A 4-m long core was extracted from a litter flat between pools in the interior of Aucayacu peatland using a Russian D-section corer with a 50-cm long chamber (Jowsey 1966; De Vleeschouwer et al. 2010; Figure 2). Core samples were transported to the laboratory at the University of Leeds, UK, and stored in refrigeration at 4°C. Three AMS ^{14}C dates were retrieved from sieved acid-alkali-acid treated peat with rootlets picked out. ^{14}C dating was carried out at NERC Radiocarbon Facility (East Kilbride) and dates were calibrated using IntCal13 (Reimer et al. 2013). Testate amoebae were prepared using a modified version of Booth et al. (2010). As testate amoebae were extremely rare at depth in the core material, a fine sieve of 35 μm was used instead of the standard 15 μm to improve sample clarity. No small specimens were found in the <35 μm fraction. Samples were stored in deionised water before analysis. Testate amoebae were counted under transmitted light at 200-400× magnification and identified using test morphology, composition, size and colour to distinguish taxa following Ogden and Hedley (1980), Charman et al., (2000), Meisterfeld (2000a,b), and Mazei and Tsyganov (2006). The taxonomy uses a morpho-species approach in some circumstances, where a name that includes several species has been classed as a "type". A count of at least 50 specimens was achieved for all samples. The weighted-averaging partial least squares (component 3) transfer function of Swindles et al. (2014) was applied to the subfossil testate amoebae to generate a water-table reconstruction. This model has the following performance statistics: $r^2_{(apparent)} = 0.81$; RMSE = 3.81; $r^2_{(leave\text{-}one\text{-}out\ cross\ validation)} = 0.65$, RMSEP = 5.24, water-table depth range = 49 to -12 cm. As the transfer function is based on one-time water table measurements the reconstruction was detrended by linear regression following Swindles et al. (2015). Peat loss-on-ignition and humification were determined following Chambers et al. (2011) and Roos-Barraclough et al. (2004), respectively. Humification determinations were carried out on the same samples as those analysed for testate amoebae. Statistical analyses were carried out using C2 (Juggins, 2007) and R v. 3.1.2 (R Core Team, 2014).

Results and Discussion

Testate amoebae were in extremely low abundance in the core, which may be related to relatively poor preservation (Swindles and Roe, 2007; Mitchell et al., 2008). However, a count of 50 or more was achieved in all cases (Figure 3). Payne and Mitchell (2009) showed that meaningful palaeoenvironmental signals can still be obtained from testate amoebae with counts as low as 50 specimens. The transfer function was applied to the subfossil data and there were no missing modern analogues. The subfossil testate amoebae diagram (Figure 3) was zoned by visual inspection as follows:

Z1 (300-180 cm) - This zone is characterised by a high relative abundance of *Hyalosphenia subflava* (major and minor). *Phryganella acropodia* occurs up to the middle of the zone. *Centropyxis aculeata* appears in the bottom of the zone and in the top – suggesting wet conditions at this time. The total number of taxa fluctuates but remains below 10. The water table depth curve exhibits a humpbacked profile changing from ~0 to 10 cm, and then getting wetter again towards the top of the zone.

Z2 (180-120 cm) – The number of taxa increases slightly in this zone. *Hyalosphenia subflava* "major" has a similar percentage to zone Z1; however, *H. subflava* "minor" decreases considerably. *Centropyxis aculeata* reaches ~20%, but disappears towards the top of the zone. Water table decreases to ~11 cm.

Z3 (120-50 cm) – The number of taxa is higher than in the former zone but fluctuates. Several new species appear such as: *Arcella arenaria*, *Argynnia caudata*, *Centropyxis aerophila*, *Difflugia pulex*, *Padaungiella langeniformis* and *Tracheleuglypha dentata*; however, none of these species are very abundant. The abundance of *Trigonopyxis arcula* "polygon aperture" increases considerably suggesting drier conditions. There is also an increase in *Phryganella acropodia*. Reconstructed water-table increased from ~11 cm to ~7 cm and then decreased to ~15 cm in top of the zone.

Z4 (50-0 cm) - Relative abundance of *Hyalosphenia subflava* (major and minor) is high (over 50%) in this zone. The percentage of *Centropyxis aculeata* increased towards the top of the peat profile, suggesting wetter conditions. Additionally *Cryptodifflugia oviformis* has a high abundance compared to the rest of the profile which may be related to better preservation at the top of the profile. *Phryganella acropodia* reached ~40 % at the top of the core which might be an artefact of better preservation in the core top. In general, the testate amoebae assemblage indicates rising water table from ~13 to 2 cm. Species diversity is also highest in this zone – providing evidence that the lower levels are being affected by poor preservation. One specimen of the new species *Arcella peruviana* was found in this zone (Reczuga et al., 2015).

The relationship between selected species of modern testate amoebae and water-table depth in Aucayacu peatland is shown in Figure 4 (data are from Swindles et al., 2014). It is apparent that the species *Centropyxis aculeata* is an important indicator of near-surface water tables, supporting previous observations (e.g. Charman et al., 2000 and references therein). The relationship between water-table depth and the abundance of the other taxa is more ambiguous. There is general agreement between the level of humification and testate amoeba-derived water-table reconstruction (r = -0.48, $p < 0.05$, $n = 25$) (Figure 5), suggesting that both proxies are responding to a common hydrological driver. Radiocarbon dating shows that the peatland began to develop ~ 7700 cal. BP and was characterised by near-surface water tables, potentially as a swamp (Figure 5). The peatland then became drier as the peat dome developed before entering a phase at ~ 6400 cal. BP characterised by a wetter peat surface driven by high river levels. Flooding at this time is indicated by supressed loss-on-ignition values associated with increased deposition of minerogenic material. There is also a shift to increased surface wetness near the top of the profile that may relate to recent increased wetness in western Amazonia (Gloor et al., 2013). However, further detailed dating of the recent peats is needed to clarify this.

Tropical peatlands are globally-important climate carbon stores (Page et al., 2011) that are under threat from human impacts and climate change. However, there is a lack of information regarding the ecohydrological dynamics and Holocene development pathways of these systems. Our work shows that even highly degraded, low-abundance assemblages of testate amoebae can be recovered from tropical peats and provide important paleoecohydrological information. While subfossil testate amoebae in tropical peatlands may never provide the level of information that can be gained from mid-high latitude peatlands they nonetheless provide insight into the hydrological variability of tropical peatlands that needs to be considered in global climate models and feedback mechanisms. This information alongside other proxy evidence, e.g., pollen (plant functional types), humification (degree of decomposition), bulk density (carbon and peat accumulation) is important for testing the outputs of peatland development models (Frolking et al., 2010; Morris et al., 2011; Swindles et al., 2012) modified for tropical peatland ecosystems. In the case of Amazonian peatlands, testate amoebae also provide information regarding long-term hydrological change and floodplain dynamics in Amazonia (Figure 5).

Conclusions

[1] Testate amoebae were analysed in a core from a tropical peat dome in western Amazonia (Peru). Subfossil tests were sparse, although a minimum count of 50 specimens was achieved for each sample.

[2] The most abundant testate-amoeba taxa in the core include *Centropyxis aculeata, Hyalosphenia subflava, Phryganella acropodia* and *Trigonopyxis arcula*. *Centropyxis*

aculeata is an important indicator of standing water in tropical peatlands. A transfer function developed from the same site was applied to the subfossil assemblages to reconstruct fluctuations in water-table depth from ~7700 cal. BP to present.

[3] Our work shows that testate amoebae can provide useful information regarding ecohydrological changes in tropical peatlands during the Holocene, despite the problems of low abundance and poor preservation.

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Figure captions

Figure 1. Map showing the location of the Aucayacu peatland, Loreto region, Peruvian Amazonia. False colour Landsat TM RGB image (Orthorectified, WRS-2, Path 007, Row 063). Band 4 was assigned to red, band 5 was assigned to green and band 7 was assigned to blue. Landsat Data are available from the U.S. Geological Survey (http://earthexplorer.usgs.gov/).

Figure 2. Photographs of (A) Pole forest typical of the Aucayacu peatland; (B) Dry 'litter flat' area; (C) Peat pool.

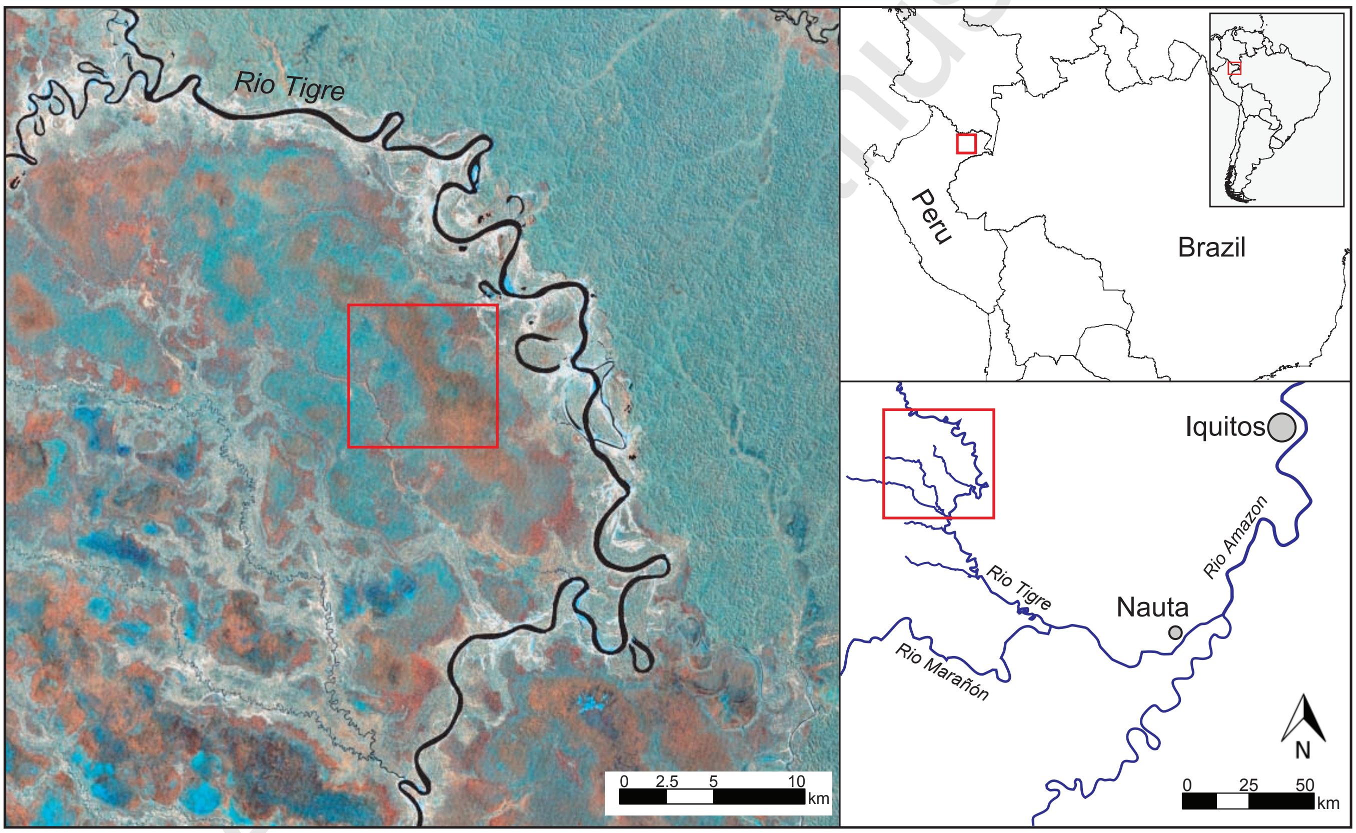
Figure 3. Relative abundance of subfossil testate amoeba preserved in the Aucayacu core. Also shown are the total count of tests, number of slides analysed to achieve the total count, the number of taxa in each sample, Shannon diversity index, water-table depth reconstruction (with errors derived from bootstrapping), and the water-table depth residuals (detrended following Swindles et al., 2015).

Figure 4. Contemporary hydrological distribution of selected testate amoeba species present in the Aucayacu core. The data are from Swindles et al. (2014). The red line represents calculated optima from a simple Gaussian species packing model, based on weighted averaging (ter Braak and van Dam, 1989); the thin blue lines represent the tolerance (standard deviation).

Figure 5. Detrended water-table depth reconstruction, plotted alongside humification (% transmission) and loss-on-ignition data. Radiocarbon dates and hydrological interpretations are illustrated.

Table 1. Taxa names and taxonomic authorities. All taxa shown are from the contemporary training set from Aucayacu (Swindles et al., 2014). Those marked with an asterisk (*) were found in the Aucayacu core samples.

Table 2. ^{14}C dates. AMS 14C dates calibrated using IntCal13 (Reimer et al., 2013), including 2σ calibrated ages.


Rio Tigre
0 2.5 5 10
km
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Iquitos
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Rio Tigre
Nauta
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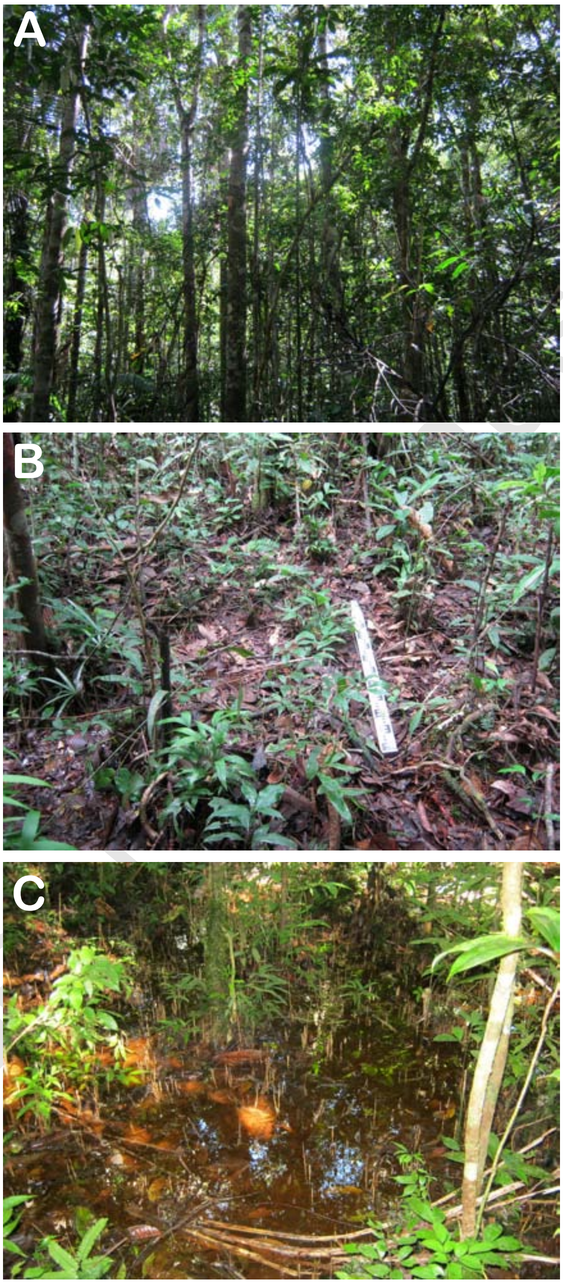
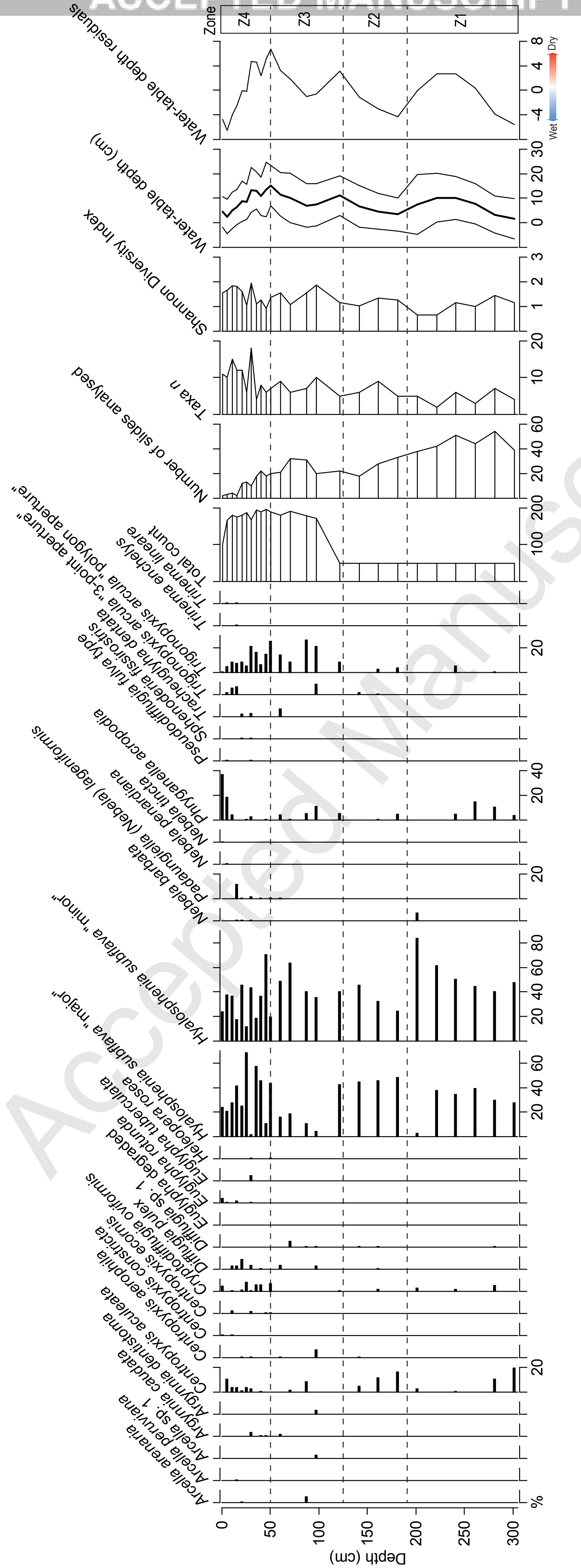
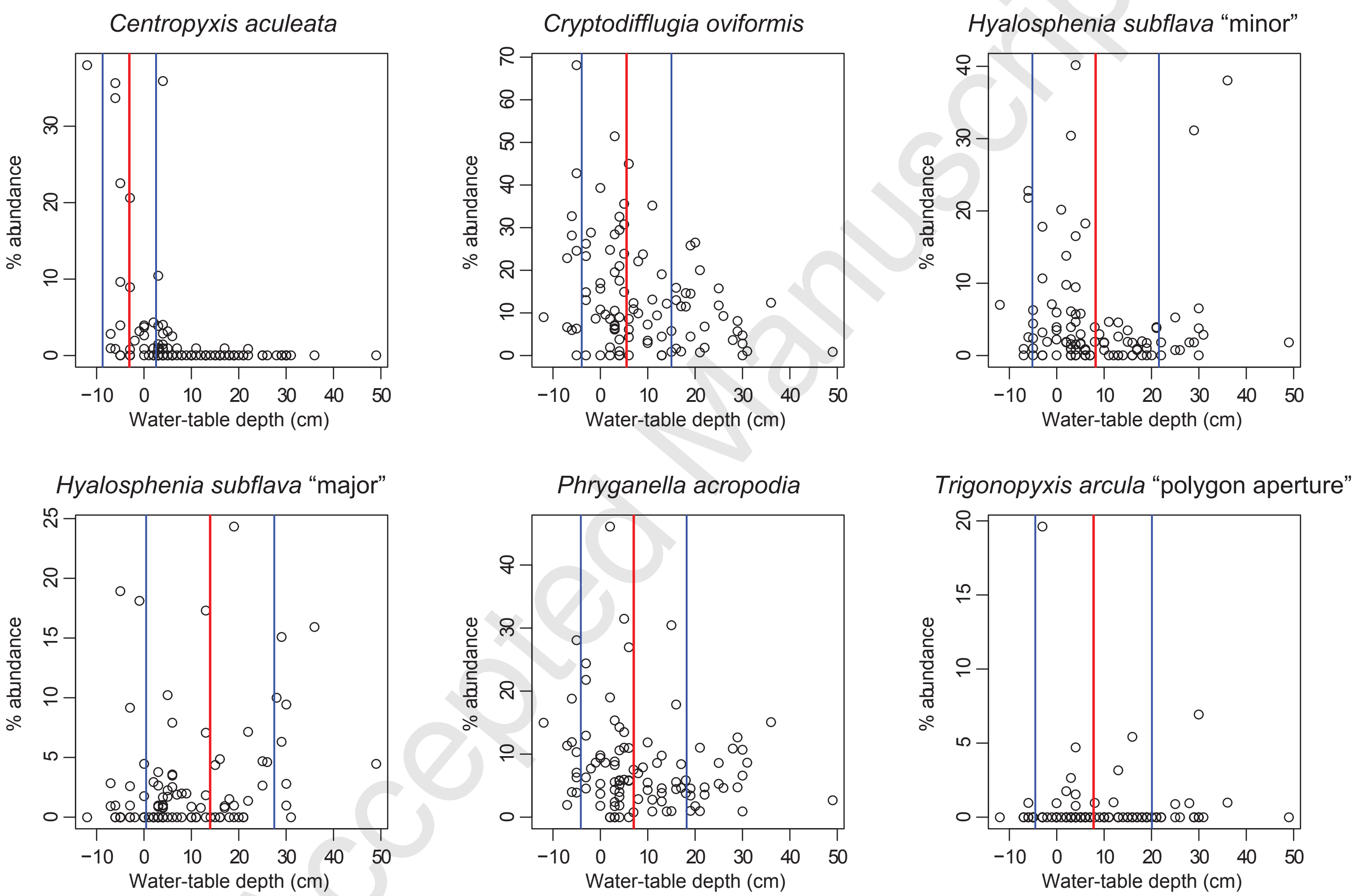
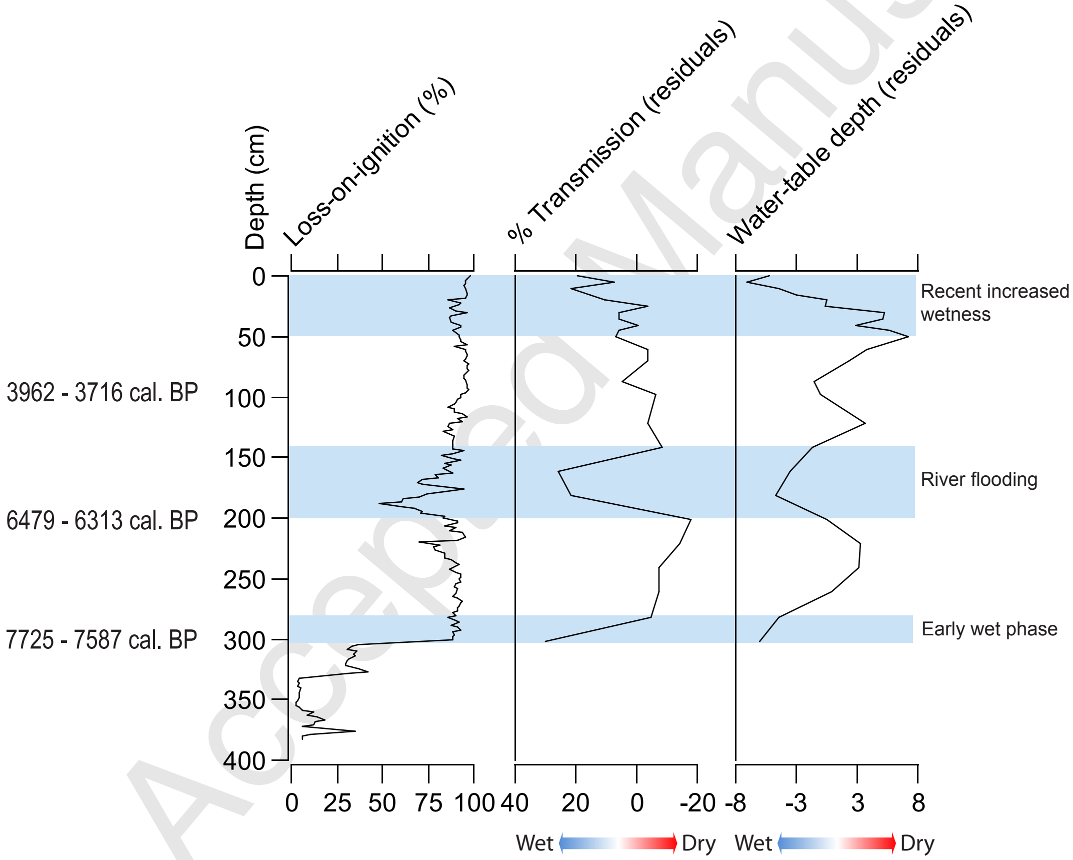

A
B
C

Figure 3



Zone
Z4
Z3
Z2
Z1
Water-table depth residuals
Dry
Wet
Water-table depth (cm)
Shannon Diversity Index
Taxa n
Number of slides analysed
Total count
Trinema lineare
Trinema enchelys
Trigonopyxis arcula "polygon aperture"
Trigonopyxis arcula "3-point aperture"
Tracheuglypha dentata
Sphenoderia fissirostris
Pseudodifflugia fulva type
Phryganella acropodia
Nebela tincta
Nebela penardiana
Padaungiella (Nebela) lageniformis
Nebela barbata
Hyalosphenia subflava "minor"
Hyalosphenia subflava "major"
Heleopera rosea
Euglypha tuberculata
Euglypha rotunda
Euglypha degraded
Euglypha sp. 1
Difflugia pulex
Difflugia oviformis
Cryptodifflugia oviformis
Centropyxis ecornis
Centropyxis constricta
Centropyxis aerophila
Centropyxis aculeata
Argynnia dentistoma
Argynnia caudata
Arcella sp. 1
Arcella peruviana
Arcella arenaria
%
Depth (cm)


Centropyxis aculeata
Cryptodifflugia oviformis
Hyalosphenia subflava "minor"
Hyalosphenia subflava "major"
Phryganella acropodia
Trigonopyxis arcula "polygon aperture"
% abundance
Water-table depth (cm)
−10
0
10
20
30
40
50



Depth (cm)
Loss-on-ignition (%)
% Transmission (residuals)
Water-table depth (residuals)
3962 - 3716 cal. BP
6479 - 6313 cal. BP
7725 - 7587 cal. BP
0
50
100
150
200
250
300
350
400
0 25 50 75 100
40 20 0 -20
-8 -3 3 8
Wet
Dry
Wet
Dry
Recent increased wetness
River flooding
Early wet phase

SYSTEMATIC PALAEONTOLOGY

Species name	**Authority**
*Arcella arenaria**	Greef 1866
*Arcella peruviana**	Reczuga *et al.* 2015
Arcella spp.*	n/a
*Argynnia caudata**	Leidy 1879
*Argynnia dentistoma**	Penard 1890
Argynnia spicata	Wailes 1913
Assulina muscorum	Greeff 1888
*Centropyxis aculeata**	Ehrenberg 1838
*Centropyxis aerophila**	Deflandre 1929
*Centropyxis constricta**	Ehrenberg 1841
*Centropyxis ecornis**	Ehrenberg 1841
*Cryptodifflugia oviformis**	Penard 1890
Cryptodifflugia oviformis “narrow”	Penard 1890
*Difflugia pulex**	Penard 1902
Difflugia spp.*	n/a
Euglypha crenulata	Wailes 1912
Euglypha cristata	Leidy 1874
Euglypha degraded*	n/a
Euglypha rotunda type*	Wailes and Penard 1911
Euglypha strigosa	(Ehrenberg 1872); Leidy 1878
*Euglypha tuberculata**	Dujardin 1841
*Heleopera rosea**	Penard 1890
Heleopera sylvatica	Penard 1890
Hyalosphenia subflava “major”*	Cash and Hopkinson 1909
Hyalosphenia subflava “minor”*	Cash and Hopkinson 1909
Lesqueresia spiralis	Ehrenberg 1840
*Nebela barbata**	Leidy 1874
Nebela militaris	Penard 1890
*Nebela penardiana**	Deflandre 1936
*Nebela tincta**	(Leidy 1979); Awerintzew 1906
*Padaungiella (Nebela) lageniformis**	(Penard 1890); Lara et Todorov
Padaungiella (Nebela) tubulata	(Brown 1911); Lara et Todorov
Phryganella acropodia type*	(Hertwig and Lesser 1874); Cash and Hopkinson 1909
Physochila cratera	Wailes 1912
Physochila griseola	Wailes and Penard 1911
Pseudodifflugia fulva type*	Archer 1870
Pyxidicula operculata	Ehrenberg 1838
Quadrulella symmetrica	(Wallich 1863); Schulze 1875
*Sphenoderia fissirostris**	Schlumberger 1845
Tracheolocorythion pulchellum	Penard 1890
*Tracheleuglypha dentata**	Deflandre 1929
Trigonopyxis arcula “3-point aperture”*	Penard 1912
Trigonopyxis arcula “polygon aperture”*	Penard 1912
Trinema complanatum	Penard 1890
*Trinema enchelys**	Leidy 1878
Trinema grandis	Chardez 1960
*Trinema lineare**	Penard 1890

Code	Depth	Conventional ^{14}C age (years BP ± 1σ)	Material	$\delta^{13}C_{VPDB}$ ± 0.1	Carbon content (% by weight)	Calibrated age (2σ)
SUERC-59689	90 - 91 cm	3549 ± 37	Peat, sieved and roots removed	-29.4	58.3	3962 - 3716 cal. BP (Median probability = 3842 cal. BP)
SUERC-59691	200 - 201 cm	5625 ± 37	Peat, sieved and roots removed	-29.8	52.1	6479 - 6313 cal. BP (Median probability = 6404 cal. BP)
SUERC-59693	300 - 301 cm	6825 ± 39	Peat, sieved and roots removed	-29.9	14.7	7725-7587 cal. BP (Median probability = 7656 cal. BP)