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Response of testate amoebae to a late Holocene ecosystem shift in an Amazonian peatland

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Abstract

To date there have only been two studies using testate amoebae as palaeoecological indicators in tropical peatlands. Here we present a new ~500-year testate amoeba record from San Jorge, a domed peatland in Peruvian Amazonia, which has a well-constrained vegetation history based on pollen analysis. We observe a major shift from *Hyalosphenia subflava* to *Cryptodifflugia oviformis*-dominated communities at ~50 cm depth (*c.* AD 1760), which suggests a change to drier conditions in the peatland. The application of a statistical transfer function also suggests a deepening of the water table at this time. The transition in the microbial assemblage occurs at a time when pollen and geochemical data indicate drier conditions (reduced influence of river flooding), leading to an ecosystem switch to more ombrotrophic-like conditions in the peatland. Our work illustrates the potential of testate amoebae as important tools in tropical peatland palaeoecology, and the power of multiproxy approaches for understanding the long-term development of tropical peatlands.

Keywords: TROPICAL PEATLANDS; TESTATE AMOEBAE; PALAEOHYDROLOGY; AMAZONIA; AMAZON RAINFOREST

Introduction

Tropical peatlands represent a carbon store of global importance and can be found in Asia, Africa, and Central and South America (Dargie et al., 2017; Page et al., 2011). In South America, the Pastaza-Marañon foreland basin (PMFB) in NW Peru represents the most carbon dense landscape in Amazonia owing to an abundance of peatlands (e.g. Draper et al., 2014), including nutrient-poor ombrotrophic peat domes and river-influenced minerotrophic peat swamps (Lähteenoja and Page, 2011). It has been estimated that peatlands of the PMFB account for 3.5% of the global tropical peatland carbon stock, cover 35,600 ± 2133 km^2 and contain 3.14 (0.44-8.15) Pg C (Draper et al., 2014). One type of ecosystem in the Pastaza-Marañon foreland basin – peatland pole forest – has been identified to be the most carbon-dense ecosystem type in the Amazon Basin (1,391 ± 710 Mg C ha^{-1}) once below ground carbon stocks are taken into account (Draper et al., 2014). Despite the importance of this ecosystem type, to date there have only been two studies examining the long-term development of pole-forest peatlands in Amazonia (Kelly et al., 2017; Swindles et al., in press).

Peatlands in Amazonia have so far escaped the widespread damage seen in Southeast Asia, but are nevertheless threatened by human activities including drainage, deforestation, mining, agricultural expansion and infrastructure projects (Householder et al., 2012; Roucoux et al., 2017). Although tropical peatlands are behaviourally similar to northern peatlands in many ways (University of Leeds Peat Club, 2017), studies of their hydrology have shown that tropical peatlands can have high hydraulic conductivities (Baird et al., 2017; Kelly et al., 2014), potentially making them vulnerable to rapid carbon loss when drained or if hydrological boundary conditions are altered by natural processes.

Testate amoebae (TA) can be sensitive wetness indicators and have become a standard tool for hydrological reconstruction in northern peatlands (e.g. Amesbury et al., 2006; Charman and Warner 1992; Swindles et al., 2009). However, TA have only been used as hydrological indicators in one Amazonian peatland to date – Aucayacu, a nutrient-poor peat dome in Peruvian Amazonia (Reczuga et al., 2015; Swindles et al., 2014, 2016, in press). A statistical transfer function has been developed from this site that can be used for long-term reconstruction of water-table depth down-core (Swindles et al., 2014). Despite problems of poor preservation and low concentration of TA in some tropical peats, it has been demonstrated that the approach can be used to infer major palaeohydrological shifts through time (Swindles et al., 2016). However, this method needs to be tested further in other tropical peatlands in Amazonia and beyond (e.g. Biagioni et al., 2015). In this study we test the response of TA to an ecosystem shift reconstructed using pollen and geochemical analyses at San Jorge, an ombrotrophic domed peatland bordering the Amazon River in Peruvian Amazonia (Fig. 1).

Materials and methods

San Jorge peatland is located in one of the wettest parts of Amazonia with a total annual rainfall exceeding 3000 mm, and remaining above 100 mm per month even in the dry season (Marengo 1998). Mean annual temperature is c. 25˚C, with high relative humidity of 80–90 % throughout the year (Marengo 1998). The vegetation of the core site is characterised by 'pole' forest (Draper et al., in press), dominated by three species: *Pachira* aff. *brevipes* (A. Robyns) W.S Alverson (Malvaceae), *Remijia* aff. *ulei* K. Krause (Rubiaceae), and *Calophyllum brasiliense* Cambess (Clusiaceae) (Kelly et al., 2014); *Mauritia flexuosa*-dominated palm swamp occurs towards the margins of the peatland.

The peatland was sampled in 2010 using a Russian peat corer (e.g. De Vleeschouwer et al., 2010) at location 4°03′48″ S, 73°11′42″ W. Detailed pollen analysis has previously been undertaken on the core and supplemented with loss-on-ignition, C/N and geochemical analyses (Kelly et al., 2017). Chronological control was achieved using a combination of ^{14}C and ^{210}Pb dating (Tables 1 and 2; Kelly et al., 2017). A Bayesian age-depth model incorporating the ^{210}Pb and ^{14}C dates was produced using the BACON package (Blaauw and Christen, 2011). For the purpose of this study TA were extracted from the peat samples in the top 1-m of the peat core (which spans the ecological transition of interest). Prior to analysis testate amoebae were stored in refrigeration at 4ºC and analysed in 2012 (2 years after the field campaign). This was achieved by sieving at 300 μm and back-sieving at 15 μm following Booth et al., (2010). TA were counted under transmitted light at 200–400× magnification and were identified using morphology, composition, size and colour to distinguish taxa. At least 100 specimens were counted (*n* = 101–186) in each sample to ensure statistical reliability (e.g. Patterson and Fishbein 1989). TA were identified using several sources (Charman et al., 2000; Mazei et al., 2006; Meisterfeld, 2000ab; Ogden and Hedley, 1980; Siemensma, 2018). The taxonomy used a morphospecies approach in certain circumstances, where a designation that includes other species or several morphotypes is referred to as a "type" (e.g. Mitchell et al., 2014). The weighted averaging partial least-squares (WA-PLS) transfer function (component 3) of Swindles et al. (2014) was applied to the TA data and sample-specific errors of prediction were calculated from 999 bootstrap cycles. Weak silicic idiosomic tests that do not preserve well in peatlands were removed before running the reconstruction (Euglypha, Trinema and Tracheleuglypha spp.) (e.g. Swindles and Roe, 2007). Detrended Correspondence Analysis (DCA) was carried out and axis one scores were used as a one-dimensional summary of the major changes in the assemblages. The Shannon Diversity Index (SDI) was also calculated for each sample to examine diversity down-core.

Results

A total of 33 TA taxa from 16 genera were identified in the San Jorge peat core (Table 3; Fig. 2). The most abundant taxa in the core include *Hyalosphenia subflava* "minor" (< 60 µm length) and *Hyalosphenia subflava* "major" (> 60 µm length), *Cryptodifflugia oviformis*, *Phryganella acropodia* and *Trigonopyxis arcula* "polygon aperture". Shannon diversity and richness decrease down-core suggesting poorer preservation of some taxa in the deeper levels. In particular, taxa with idiosomic siliceous tests (*Euglypha*, *Tracheleuglypha* and *Trinema* spp.) disappear down-core, which is likely related to poor preservation (e.g. Swindles and Roe 2007).

A major shift from an assemblage dominated by *Hyalosphenia subflava* to one dominated by *Cryptodifflugia oviformis* occurs around 50 cm (*c.* AD 1760), suggesting a change to drier conditions. This is also demonstrated by the DCA axis 1 score and water table reconstruction (Fig. 2). The pollen zones of Kelly et al., (2017) are indicated on the diagram (Fig. 2). When the average reconstructed water table is calculated for each zone, a clear shift to drier conditions is observed between zones SJ-4 and SJ-5. A shift to slightly wetter conditions in the most recent period may be suggested by the appearance of the unambiguous wet indicator *Centropyxis aculeata* at the very top of the core (Fig. 2).

Discussion

The hydrological change to drier conditions at around 50 cm in the water-table reconstruction (derived from the Aucayacu transfer function) emerges as a result of the change in dominant species from *Hyalosphenia subflava* "major" (optimum = 2.3 cm, *n* samples = 63) to *Cryptodifflugia oviformis* (optimum = 5.2 cm, *n* samples = 51) (Swindles et al., 2014). In the Aucayacu peatland, *Hyalosphenia subflava* "major" is a relatively wet indicator which contrasts the ecology of *Hyalosphenia subflava* in Northern peatlands, where it is almost always an unambiguous dry indicator (e.g. Turner and Swindles, 2012). *Hyalosphenia subflava* "minor" is a drier indicator in Aucayacu (optimum = 9.2 cm) than *Hyalosphenia subflava* "major". The change in assemblage occurs across the SJ-4 – SJ-5 pollen assemblage zone (PAZ) boundary (indicating a significant change in vegetation composition) (Kelly et al., 2017), and coincides with decreases in both C/N and Ca/Mg ratios. (Fig. 3). The transition from PAZ SJ-4 to SJ-5 is characterised by a decrease in abundance of open canopy indicators (fern spores) and palm swamp indicators (*Euterpe*-t., *Ilex* sp., and *Mauritia flexuosa*), and an increase in the relative abundance of peatland pole forest indicators (*Mauritiella* sp. and *Maouetia* sp.) (Kelly et al., 2017). Taken together with the pattern of decreasing C/N and Ca/Mg ratios, this interval is interpreted to represent the transition from flooded minerotrophic palm swamp to raised ombrotrophic pole forest with little or no flooding (Kelly et al., 2017). The shift towards drier conditions indicated by the TA-based water table reconstruction is consistent with this interpretation. There is good correspondence between C/N data and the testate amoeba-derived water-table reconstruction which may reflect changing peat humification, which itself is strongly influenced by hydrological conditions on the peatland surface (Fig. 3).

In the top-most 5cm of the San Jorge record, the TA data show a shift to wetter conditions occurring in recent decades. This was also observed in Aucayacu peatland record (located 130 km to the west) and may be related to the development of a wetter climate in this region (Swindles et al., in press). There is some support for this from modern climatic observations; collated rainfall and runoff data show an increase in precipitation in recent decades, particularly in the wet season (Gloor et al., 2013). It would appear that peatland hydrology could be responding to the intensification of the hydrological cycle seen in recent decades, although further analysis of records from different sites is required to substantiate this (Swindles et al., in press).

These new data from San Jorge add to a growing body of work to suggest that TA can be sensitive indicators of ecosystem and hydrological change in tropical peatlands, just as in northern peatlands (Bagioni et al., 2015; Swindles et al., in press). However, problems may arise in deeper/older peats including the low concentration of tests and poor preservation (e.g. Swindles et al., 2016). Much remains unknown about the microbial ecology of tropical wetlands (Patterson et al., 2015), and particularly peatlands (e.g. Reczuga et al., 2015; Swindles et al., 2014). Future studies should prioritise the characterization of TA communities from contrasting tropical peatlands in South and Central America, Africa and SE Asia to examine the wide-scale variations in biogeography and TA autecology. The combination of testate amoeba and pollen data provide a particularly powerful tool for investigating Holocene ecohydrological changes in Amazonian peatlands.

Amazonian peatlands are important in terms of ecosystem services, carbon storage and biodiversity, and represent important archives of past climatic, ecological and environmental information (Kelly et al., 2017; Swindles et al., 2014, in press; Watson et al., 2015). Perhaps uniquely for Amazonian ecosystems, peatlands create a detailed record of their own history which can be used to test hypotheses developed from modern ecological observations, for example, the effect of ecosystem longevity on modern species diversity, using palaeoecological data (e.g. Draper et al., 2017). However, Amazonian peatlands are threatened by the expansion of commercial agriculture and infrastructure projects (e.g. Roucoux et al., 2017). Policies should focus on the conservation of these important ecosystems and carbon stores.

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Figure captions

Fig. 1. The location of the San Jorge peatland in Peruvian Amazonia. Maps are from Google Earth (2016).

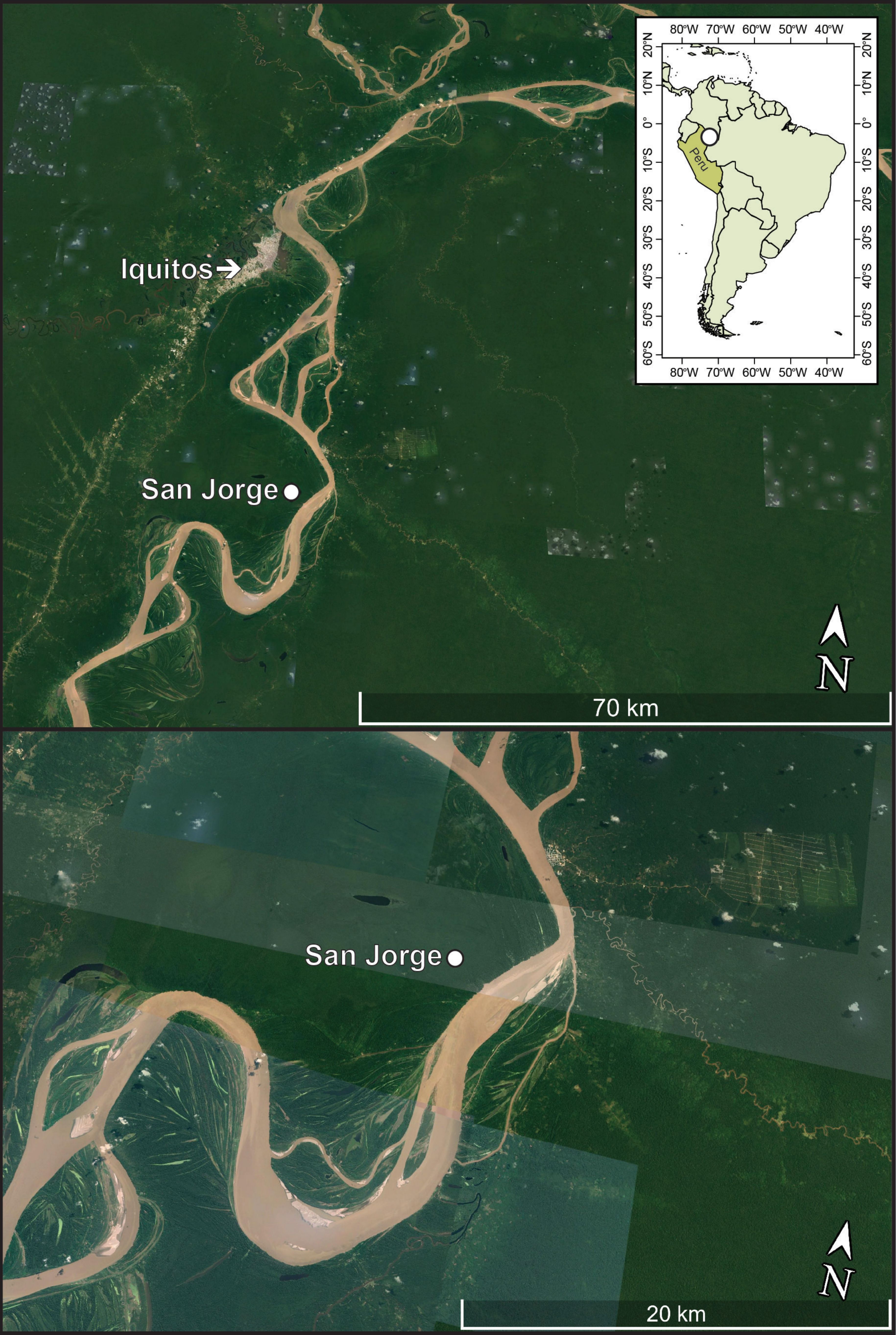
Fig. 2. Percentage testate amoeba data from the San Jorge peat core. Total count, Shannon Diversity Index, DCA axis 1 score and the water-table reconstruction are also shown. Errors on the water-table reconstruction were generated through 999 bootstrap cycles. The age model from Kelly et al., (2017) is plotted on a secondary y-axis. Average water-table depth for the pollen assemblage zones (PAZ) SJ-4 and SJ-5 (defined in Kelly et al., 2017) are also illustrated. The taxa shaded in orange were removed before carrying out the water-table

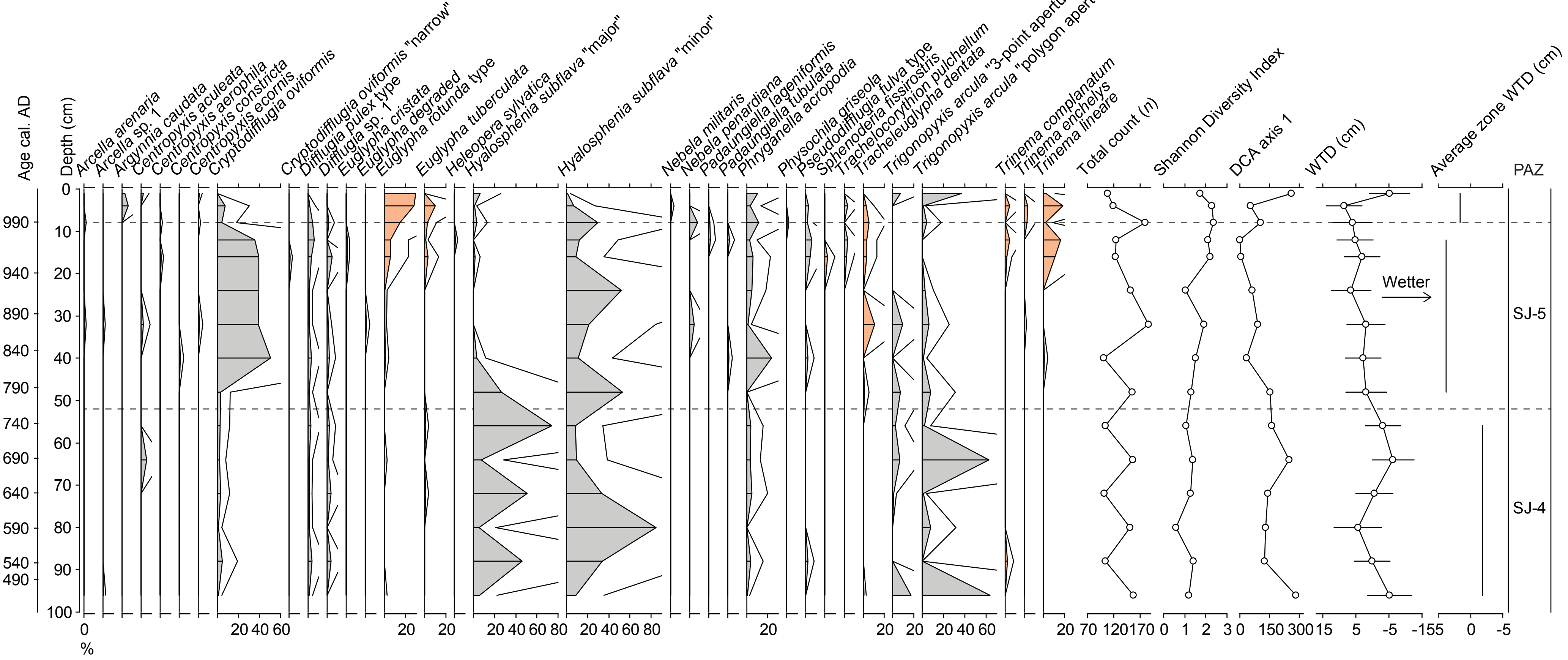
reconstruction. 5× exaggeration lines are shown to highlight minor taxa. Negative water-table depths indicate above-surface water.

Fig. 3. Selected pollen and other environmental data from the San Jorge core plotted with the water-table depth reconstruction. Negative water-table depths indicate above-surface water.

Highlights

Testing testate amoeba response to an ecosystem shift in an Amazonian peatland
A transition from dominance of *Hyalosphenia subflava* to *Cryptodifflugia oviformis*
The shift occurs at a time when pollen and geochemical data indicate drier conditions
We illustrate the potential of testate amoebae in tropical peatland palaeoecology


Iquitos
San Jorge
80°W 70°W 60°W 50°W 40°W
20°N
10°N
0°
10°S
20°S
30°S
40°S
50°S
60°S
Peru
N
70 km
San Jorge
N
20 km


Age cal. AD
Depth (cm)
Arcella arenaria
Arcella sp. 1
Argynnia caudata
Centropyxis aculeata
Centropyxis aerophila
Centropyxis constricta
Centropyxis ecornis
Cryptodifflugia oviformis
Cryptodifflugia oviformis "narrow"
Difflugia pulex type
Difflugia sp. 1
Euglypha cristata
Euglypha degraded
Euglypha rotunda type
Euglypha tuberculata
Heleopera sylvatica
Hyalosphenia subflava "major"
Hyalosphenia subflava "minor"
Nebela militaris
Nebela penardiana
Padaungiella lageniformis
Padaungiella tubulata
Phryganella acropodia
Physochila griseola
Pseudodifflugia fulva type
Sphenoderia fissirostris
Tracheleuglypha dentata
Trachelocorythion pulchellum
Trigonopyxis arcula "3-point aperture"
Trigonopyxis arcula "polygon aperture"
Trinema complanatum
Trinema enchelys
Trinema lineare
Total count (n)
Shannon Diversity Index
DCA axis 1
WTD (cm)
Average zone WTD (cm)
PAZ
1990
1940
1890
1840
1790
1740
1690
1640
1590
1540
1490
0
10
20
30
40
50
60
70
80
90
100
Wetter
SJ-5
SJ-4
0
%
20 40 60
20
20
20 40 60 80
20 40 60 80
20
20
20
20 40 60
20
70 120 170
0 1 2 3
0 150 300
15 5 -5 -15
5 0 -5

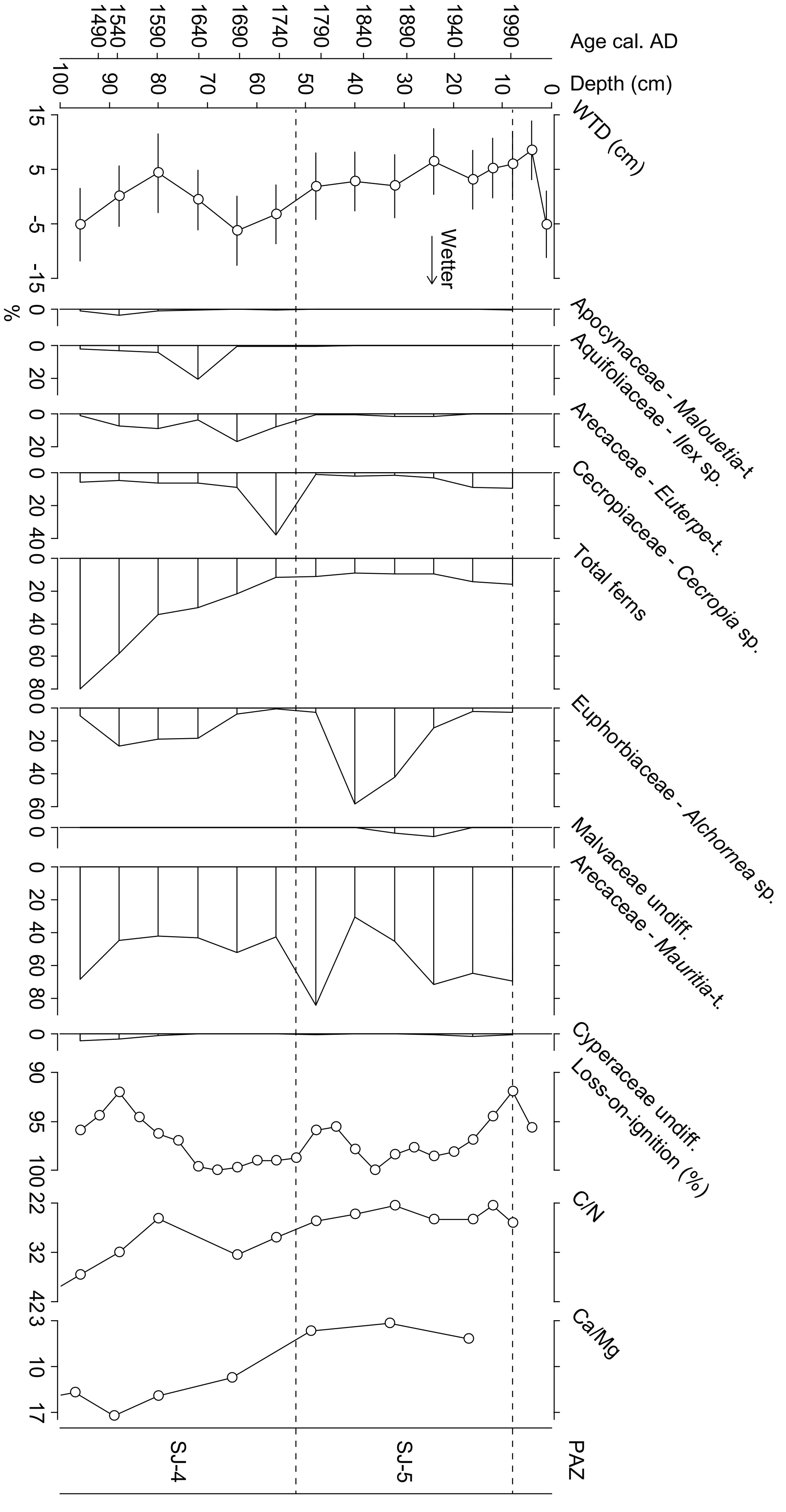

Age cal. AD
1490
1540
1590
1640
1690
1740
1790
1840
1890
1940
1990
Depth (cm)
100
90
80
70
60
50
40
30
20
10
0
WTD (cm)
15
5
-5
-15
Wetter
%
Apocynaceae - Malouetia-t
Aquifoliaceae - Ilex sp.
Arecaceae - Euterpe-t.
Cecropiaceae - Cecropia sp.
Total ferns
Euphorbiaceae - Alchornea sp.
Malvaceae undiff.
Arecaceae - Mauritia-t.
Cyperaceae undiff.
Loss-on-ignition (%)
C/N
Ca/Mg
PAZ
SJ-4
SJ-5

Table 1. Radiocarbon determinations for the San Jorge core. AMS radiocarbon dates were obtained from the NERC facility at East Kilbride (SUERC prefix) and at the ^{14}Chono radiocarbon laboratory (Queen's University Belfast; UBA prefix). Calibration was undertaken using the INTCAL13 curve. All samples are the <180 µm peat fraction. Sample UBA-20285 was a humic acid extraction.

Laboratory code	**Depth (cm)**	**^{14}C age (yrs BP)**	**Error (1σ)**	**δ^{13}C**	**Calibrated 2σ age (cal yr BP)**
UBA-20285	90–92	282	± 22	- 31.8	299–425
SUERC-54417	112–114	1623	± 41	- 29.0	1416–1564
SUERC-54418	144–146	1759	± 41	- 28.9	1610–1720
SUERC-54419	192–194	1990	± 40	- 28.8	1897–1989
SUERC-54422	238–240	2173	± 41	- 29.5	2120–2306

Table 2. ^{210}PB activity determinations for the top 50 cm of the San Jorge core. Note that ages are given in years AD. Analytical error is shown to 1σ. Total ^{210}Pb inventory = 7274.867 Bq m^{-2}. ^{210}Pb supply rate = 226.539 Bq m^{-2}yr^{-1}.

Depth (cm)	**^{210}Pb activity (Bq kg^{-1})**	**± total**	**Dry bulk density (g cm^{-3})**	**Unsupported ^{210}Pb activity (Bq kg^{-1})**	**Cumulative unsupported ^{210}Pb inventory (Bq m^{-2})**	**Age (AD)**	**Error (yrs)**
0-2	375.34	10.86	0.125	365.77	228.68	2012	0.01
2-4	360.21	21.28	0.130	350.64	1162.45	2007	0.02
4-6	517.78	13.29	0.131	508.21	2275.79	2001	0.03
6-8	445.36	11.89	0.127	435.79	3470.06	1992	0.04
8-10	315.59	9.19	0.104	306.02	4233.24	1985	0.08
10-12	223.71	7.42	0.092	214.14	4705.94	1979	0.11
12-14	223.72	6.33	0.101	214.15	5138.44	1973	0.15
14-16	302.76	9.23	0.100	293.19	5639.13	1965	0.23
16-18	219.12	7.69	0.081	209.55	6042.17	1956	0.33
18-20	188.91	6.22	0.093	179.34	6401.17	1944	0.49
20-22	134.95	6.00	0.096	125.38	6690.37	1932	0.78
22-24	67.46	3.29	0.110	57.89	6882.54	1919	1.19
24-26	41.57	1.95	0.111	32.00	6979.25	1910	1.61
26-28	32.45	1.77	0.102	22.88	7034.67	1903	1.99
28-30	43.49	2.40	0.097	33.92	7089.14	1895	2.60
30-32	38.83	1.85	0.093	29.26	7147.55	1883	3.83
32-34	24.66	1.44	0.100	15.09	7190.38	1869	5.80
34-36	21.99	1.79	0.093	12.42	7216.01	1858	8.36
36-38	22.21	1.79	0.091	12.64	7238.89	1842	13.73
38-40	19.68	0.96	0.093	10.11	7259.85	1814	32.99
40-42	14.76	0.79	0.102	5.19	7274.87		
42-44	9.57	0.60	0.109	0.00			
44-46	10.03	0.65	0.107				
46-48	11.03	0.78	0.115				
48-50	7.68	0.76	0.117				

Table 3. Testate amoeba found in the San Jorge core.

Taxon	**Authority**
Arcella arenaria	Greeff 1866
Argynnia caudata	Leidy 1879
Centropyxis aculeata	Ehrenberg 1838
Centropyxis aerophila	Deflandre 1929
Centropyxis constricta	Ehrenberg 1841
Centropyxis ecornis	Ehrenberg 1841
Cryptodifflugia oviformis	Penard 1890
Difflugia pulex type	Penard 1902
Euglypha cristata	Leidy 1874
Euglypha rotunda type	Wailes and Penard 1911
Euglypha tuberculata	Dujardin 1841
Heleopera sylvatica	Penard 1890
Hyalosphenia subflava	Cash and Hopkinson 1909
Nebela militaris	Penard 1890
Nebela penardiana	Deflandre 1936
Phryganella acropodia	Hertwig and Lesser 1874; Cash and Hopkinson 1909
Physochila griseola	Wailes and Penard 1911
Pseudodifflugia fulva type	Archer 1870
Sphenoderia fissirostris	Schlumberger 1845
Tracheolocorythion pulchellum	Penard 1890
Tracheleuglypha dentata	Deflandre 1929
Trigonopyxis arcula	Penard 1912
Trinema complanatum	Penard 1890
Trinema enchelys	Leidy 1878
Trinema lineare	Penard 1890