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

3

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11

12 **Abstract**

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

23

24

25 **Keywords:** TROPICAL PEATLANDS; TESTATE AMOEBAE; PALAEOHYDROLOGY; AMAZONIA;

26 AMAZON RAINFOREST

27 **Introduction**

28 Tropical peatlands represent a carbon store of global importance and can be found in Asia, Africa, and Central
29 and South America (Dargie et al., 2017; Page et al., 2011). In South America, the Pastaza-Marañon foreland
30 basin (PMFB) in NW Peru represents the most carbon dense landscape in Amazonia owing to an abundance
31 of peatlands (e.g. Draper et al., 2014), including nutrient-poor ombrotrophic peat domes and river-influenced
32 minerotrophic peat swamps (Lähteenoja and Page, 2011). It has been estimated that peatlands of the PMFB
33 account for 3.5% of the global tropical peatland carbon stock, cover $35,600 \pm 2133$ km² and contain 3.14 (0.44-
34 8.15) Pg C (Draper et al., 2014). One type of ecosystem in the Pastaza-Marañon foreland basin – peatland pole
35 forest – has been identified to be the most carbon-dense ecosystem type in the Amazon Basin ($1,391 \pm 710$ Mg
36 C ha⁻¹) once below ground carbon stocks are taken into account (Draper et al., 2014). Despite the importance
37 of this ecosystem type, to date there have only been two studies examining the long-term development of pole-
38 forest peatlands in Amazonia (Kelly et al., 2017; Swindles et al., in press).

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

46 Testate amoebae (TA) can be sensitive wetness indicators and have become a standard tool for
47 hydrological reconstruction in northern peatlands (e.g. Amesbury et al., 2006; Charman and Warner 1992;
48 Swindles et al., 2009). However, TA have only been used as hydrological indicators in one Amazonian
49 peatland to date – Aucayacu, a nutrient-poor peat dome in Peruvian Amazonia (Reczuga et al., 2015; Swindles
50 et al., 2014, 2016, in press). A statistical transfer function has been developed from this site that can be used
51 for long-term reconstruction of water-table depth down-core (Swindles et al., 2014). Despite problems of poor
52 preservation and low concentration of TA in some tropical peats, it has been demonstrated that the approach
53 can be used to infer major palaeohydrological shifts through time (Swindles et al., 2016). However, this
54 method needs to be tested further in other tropical peatlands in Amazonia and beyond (e.g. Biagioni et al.,

55 2015). In this study we test the response of TA to an ecosystem shift reconstructed using pollen and
56 geochemical analyses at San Jorge, an ombrotrophic domed peatland bordering the Amazon River in Peruvian
57 Amazonia (Fig. 1).

58

59 **Materials and methods**

60 San Jorge peatland is located in one of the wettest parts of Amazonia with a total annual rainfall exceeding
61 3000 mm, and remaining above 100 mm per month even in the dry season (Marengo 1998). Mean annual
62 temperature is c. 25°C, with high relative humidity of 80–90 % throughout the year (Marengo 1998). The
63 vegetation of the core site is characterised by ‘pole’ forest (Draper et al., in press), dominated by three species:
64 *Pachira* aff. *brevipes* (A. Robyns) W.S Alverson (Malvaceae), *Remijia* aff. *ulei* K. Krause (Rubiaceae), and
65 *Calophyllum brasiliense* Cambess (Clusiaceae) (Kelly et al., 2014); *Mauritia flexuosa*-dominated palm swamp
66 occurs towards the margins of the peatland.

67 The peatland was sampled in 2010 using a Russian peat corer (e.g. De Vleeschouwer et al., 2010) at
68 location 4°03'48" S, 73°11'42" W. Detailed pollen analysis has previously been undertaken on the core and
69 supplemented with loss-on-ignition, C/N and geochemical analyses (Kelly et al., 2017). Chronological control
70 was achieved using a combination of ¹⁴C and ²¹⁰Pb dating (Tables 1 and 2; Kelly et al., 2017). A Bayesian age-
71 depth model incorporating the ²¹⁰Pb and ¹⁴C dates was produced using the BACON package (Blaauw and
72 Christen, 2011). For the purpose of this study TA were extracted from the peat samples in the top 1-m of the
73 peat core (which spans the ecological transition of interest). Prior to analysis testate amoebae were stored in
74 refrigeration at 4°C and analysed in 2012 (2 years after the field campaign). This was achieved by sieving at
75 300 µm and back-sieving at 15 µm following Booth et al., (2010). TA were counted under transmitted light at
76 200–400× magnification and were identified using morphology, composition, size and colour to distinguish
77 taxa. At least 100 specimens were counted ($n = 101–186$) in each sample to ensure statistical reliability (e.g.
78 Patterson and Fishbein 1989). TA were identified using several sources (Charman et al., 2000; Mazei et al.,
79 2006; Meisterfeld, 2000ab; Ogden and Hedley, 1980; Siemensma, 2018). The taxonomy used a morphospecies
80 approach in certain circumstances, where a designation that includes other species or several morphotypes is
81 referred to as a "type" (e.g. Mitchell et al., 2014). The weighted averaging partial least-squares (WA-PLS)
82 transfer function (component 3) of Swindles et al. (2014) was applied to the TA data and sample-specific errors

83 of prediction were calculated from 999 bootstrap cycles. Weak silicic idiosomic tests that do not preserve well
84 in peatlands were removed before running the reconstruction (*Euglypha*, *Trinema* and *Tracheleuglypha* spp.)
85 (e.g. Swindles and Roe, 2007). Detrended Correspondence Analysis (DCA) was carried out and axis one scores
86 were used as a one-dimensional summary of the major changes in the assemblages. The Shannon Diversity
87 Index (SDI) was also calculated for each sample to examine diversity down-core.

88

89 **Results**

90 A total of 33 TA taxa from 16 genera were identified in the San Jorge peat core (Table 3; Fig. 2). The most
91 abundant taxa in the core include *Hyalosphenia subflava* “minor” (< 60 µm length) and *Hyalosphenia subflava*
92 “major” (> 60 µm length), *Cryptodifflugia oviformis*, *Phryganella acropodia* and *Trigonopyxis arcula*
93 “polygon aperture”. Shannon diversity and richness decrease down-core suggesting poorer preservation of
94 some taxa in the deeper levels. In particular, taxa with idiosomic siliceous tests (*Euglypha*, *Tracheleuglypha*
95 and *Trinema* spp.) disappear down-core, which is likely related to poor preservation (e.g. Swindles and Roe
96 2007).

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

104

105 **Discussion**

106 The hydrological change to drier conditions at around 50 cm in the water-table reconstruction (derived from
107 the Aucayacu transfer function) emerges as a result of the change in dominant species from *Hyalosphenia*
108 *subflava* “major” (optimum = 2.3 cm, *n* samples = 63) to *Cryptodifflugia oviformis* (optimum = 5.2 cm, *n*
109 samples = 51) (Swindles et al., 2014). In the Aucayacu peatland, *Hyalosphenia subflava* “major” is a relatively

110 wet indicator which contrasts the ecology of *Hyalosphenia subflava* in Northern peatlands, where it is almost
111 always an unambiguous dry indicator (e.g. Turner and Swindles, 2012). *Hyalosphenia subflava* “minor” is a
112 drier indicator in Aucayacu (optimum = 9.2 cm) than *Hyalosphenia subflava* “major”. The change in
113 assemblage occurs across the SJ-4 – SJ-5 pollen assemblage zone (PAZ) boundary (indicating a significant
114 change in vegetation composition) (Kelly et al., 2017), and coincides with decreases in both C/N and Ca/Mg
115 ratios. (Fig. 3). The transition from PAZ SJ-4 to SJ-5 is characterised by a decrease in abundance of open
116 canopy indicators (fern spores) and palm swamp indicators (*Euterpe*-t., *Ilex* sp., and *Mauritia flexuosa*), and
117 an increase in the relative abundance of peatland pole forest indicators (*Mauritiella* sp. and *Maouetia* sp.)
118 (Kelly et al., 2017). Taken together with the pattern of decreasing C/N and Ca/Mg ratios, this interval is
119 interpreted to represent the transition from flooded minerotrophic palm swamp to raised ombrotrophic pole
120 forest with little or no flooding (Kelly et al., 2017). The shift towards drier conditions indicated by the TA-
121 based water table reconstruction is consistent with this interpretation. There is good correspondence between
122 C/N data and the testate amoeba-derived water-table reconstruction which may reflect changing peat
123 humification, which itself is strongly influenced by hydrological conditions on the peatland surface (Fig. 3).

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

131 These new data from San Jorge add to a growing body of work to suggest that TA can be sensitive
132 indicators of ecosystem and hydrological change in tropical peatlands, just as in northern peatlands (Bagioni
133 et al., 2015; Swindles et al., in press). However, problems may arise in deeper/older peats including the low
134 concentration of tests and poor preservation (e.g. Swindles et al., 2016). Much remains unknown about the
135 microbial ecology of tropical wetlands (Patterson et al., 2015), and particularly peatlands (e.g. Reczuga et al.,
136 2015; Swindles et al., 2014). Future studies should prioritise the characterization of TA communities from
137 contrasting tropical peatlands in South and Central America, Africa and SE Asia to examine the wide-scale

138 variations in biogeography and TA autecology. The combination of testate amoeba and pollen data provide a
139 particularly powerful tool for investigating Holocene ecohydrological changes in Amazonian peatlands.

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

148

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156

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257

258 **Figure captions**

259

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

261

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

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

269

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

272

Highlights

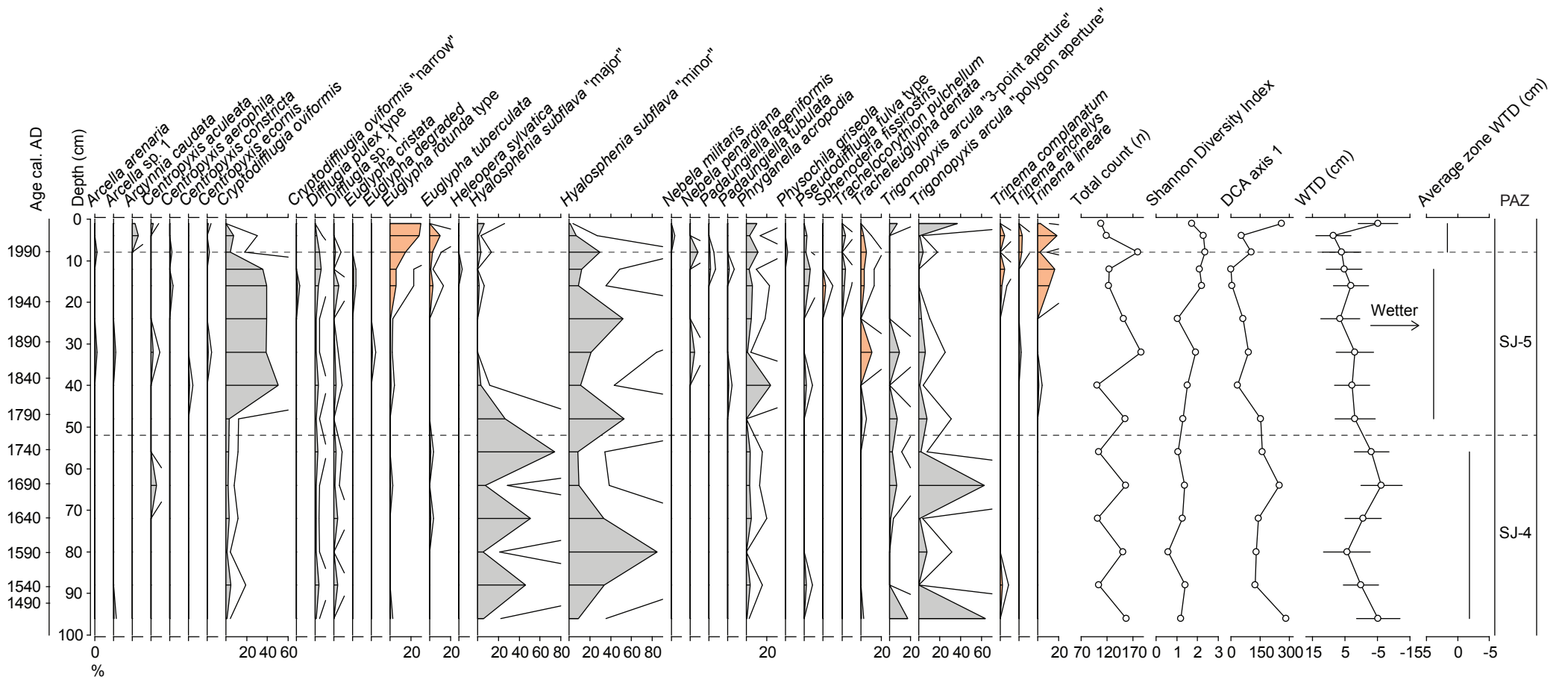
Testing testate amoeba response to an ecosystem shift in an Amazonian peatland

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





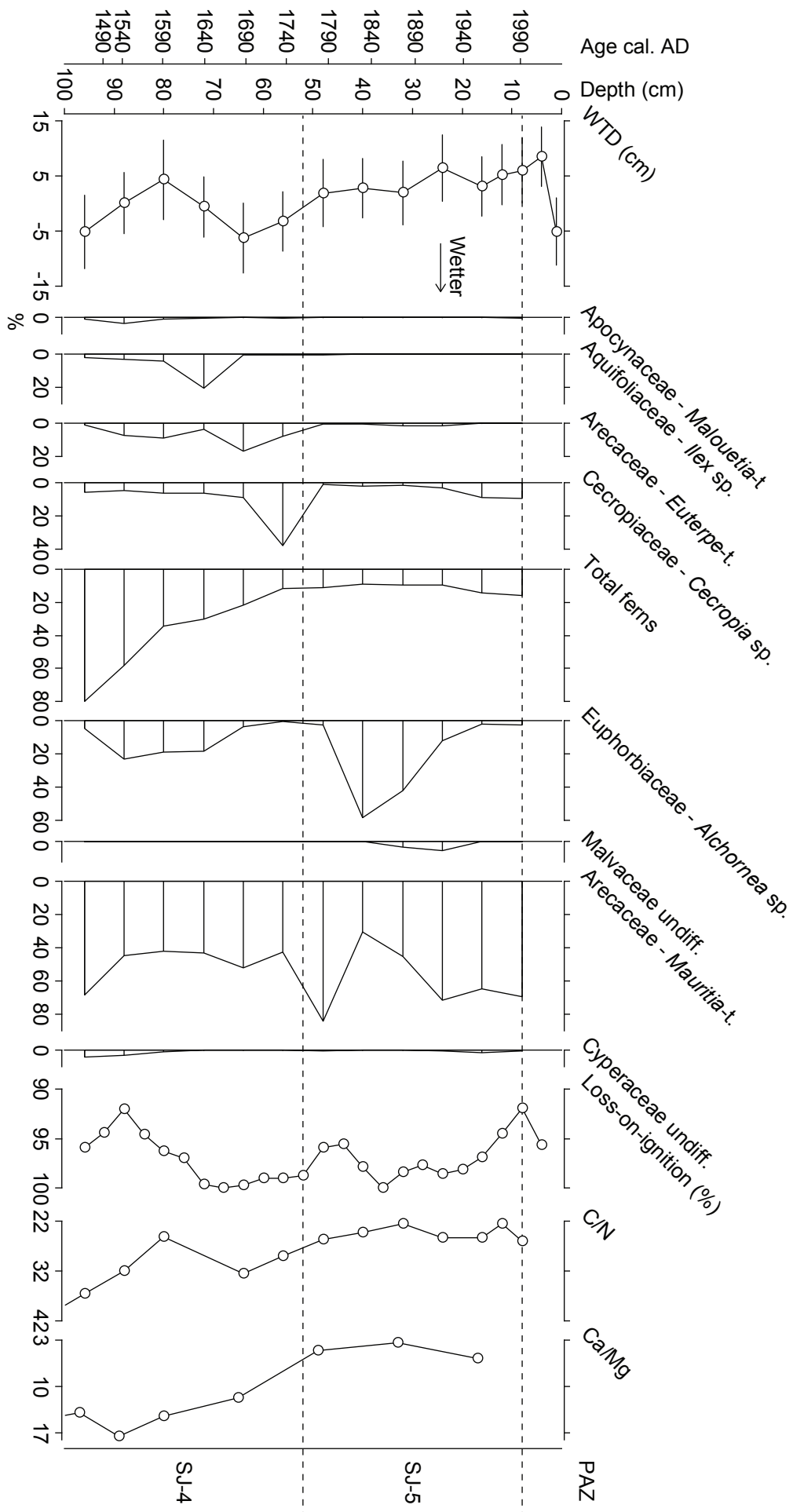


Table 1. Radiocarbon determinations for the San Jorge core. AMS radiocarbon dates were obtained from the NERC facility at East Kilbride (SUERC prefix) and at the ¹⁴Chono radiocarbon laboratory (Queen's University Belfast; UBA prefix). Calibration was undertaken using the INTCAL13 curve. All samples are 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. ²¹⁰Pb 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 ²¹⁰Pb inventory = 7274.867 Bq m⁻². ²¹⁰Pb supply rate = 226.539 Bq m⁻²yr⁻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
<i>Arcella arenaria</i>	Greeff 1866
<i>Argynnia caudata</i>	Leidy 1879
<i>Centropyxis aculeata</i>	Ehrenberg 1838
<i>Centropyxis aerophila</i>	Deflandre 1929
<i>Centropyxis constricta</i>	Ehrenberg 1841
<i>Centropyxis ecornis</i>	Ehrenberg 1841
<i>Cryptodiffugia oviformis</i>	Penard 1890
<i>Diffugia pulex</i> type	Penard 1902
<i>Euglypha cristata</i>	Leidy 1874
<i>Euglypha rotunda</i> type	Wailes and Penard 1911
<i>Euglypha tuberculata</i>	Dujardin 1841
<i>Heleopera sylvatica</i>	Penard 1890
<i>Hyalosphenia subflava</i>	Cash and Hopkinson 1909
<i>Nebela militaris</i>	Penard 1890
<i>Nebela penardiana</i>	Deflandre 1936
<i>Phryganella acropodia</i>	Hertwig and Lesser 1874; Cash and Hopkinson 1909
<i>Physochila griseola</i>	Wailes and Penard 1911
<i>Pseudodiffugia fulva</i> type	Archer 1870
<i>Sphenoderia fissirostris</i>	Schlumberger 1845
<i>Tracheolocorythion pulchellum</i>	Penard 1890
<i>Tracheleuglypha dentata</i>	Deflandre 1929
<i>Trigonopyxis arcula</i>	Penard 1912
<i>Trinema complanatum</i>	Penard 1890
<i>Trinema enchelys</i>	Leidy 1878
<i>Trinema lineare</i>	Penard 1890