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**Paper:**

Swindles, GT, Reczuga, M, Lamentowicz, M, Raby, CL, Turner, TE, Charman, DJ, Gallego-Sala, A, Valderrama, E, Williams, C, Draper, F, Honorio Coronado, EN, Roucoux, KH, Baker, T and Mullan, DJ (2014) *Ecology of testate amoebae in an Amazonian peatland and development of a transfer function for palaeohydrological reconstruction*. *Microbial Ecology: an international journal*, April . ISSN 0095-3628

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1  
2 **Ecology of testate amoebae in an Amazonian peatland and**  
3 **development of a transfer function for palaeohydrological**  
4 **reconstruction**

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6  
7 *Manuscript for MICROBIAL ECOLOGY*

- 8  
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31 Tropical peatlands represent globally important carbon sinks with a unique biodiversity and are cur-  
32 rently threatened by climate change and human activities. It is now imperative that proxy methods are  
33 developed to understand the natural ecohydrological dynamics of these systems and for testing peat-  
34 land development models. Testate amoebae have been used as environmental indicators in ecological  
35 and palaeoecological studies of peatlands, primarily in ombrotrophic *Sphagnum*-dominated peatlands  
36 in the mid- and high latitudes. We present the first ecological analysis of testate amoebae in a tropical  
37 peatland, a nutrient-poor domed bog in western (Peruvian) Amazonia. Litter samples were collected  
38 from different hydrological microforms (hummock to pool) along a transect from the edge to the interior  
39 of the peatland. We recorded 47 taxa from 21 genera. The most common taxa are *Cryptodiffugia ovi-*  
40 *formis*, *Euglypha rotunda* type, *Phryganella acropodia*, *Pseudodiffugia fulva* type and *Trinema lineare*.  
41 One species found only in the southern hemisphere, *Argygnia spicata*, is present. *Arcella* spp., *Cen-*  
42 *tropyxis aculeata* and *Lesqueresia spiralis* are indicators of pools containing standing water. Canonical  
43 Correspondence Analysis and Non-Metric Multidimensional Scaling illustrate that water table depth  
44 is a significant control on the distribution of testate amoebae, similar to the results from mid- and  
45 high latitude peatlands. A transfer function model for water table based on weighted averaging partial  
46 least-squares (WAPLS) regression is presented and performs well under cross-validation ( $r_{\text{apparent}}^2 =$   
47  $0.76$ ,  $\text{RMSE} = 4.29$ ;  $r_{\text{jack}}^2 = 0.68$ ,  $\text{RMSEP} = 5.18$ ). The transfer function was applied to a 1-m peat  
48 core and sample-specific reconstruction errors were generated using bootstrapping. The reconstruction  
49 generally suggests near-surface water tables over the last 3,000 years, with a shift to drier conditions  
50 at c. cal. AD 1218-1273.

# 51 1 Introduction

52 Peatlands are globally important ecosystems in terms of biodiversity, hydrology, and for the role they  
53 play in the carbon cycle [1]. Peatlands store approximately one third of the carbon contained in the  
54 terrestrial biosphere, whilst covering only approximately 3% of the land and freshwater surface [2].  
55 There is much concern over the status of global peatlands as they are threatened by climate change,  
56 pollution and other human impacts such as peat cutting, drainage and deforestation. Peatlands can  
57 be considered to be ecohydrological systems as there are linkages and feedbacks between climate, hy-  
58 drology, chemistry and nutrients, and plant and microbial communities [3]. There is often marked  
59 variation across the surfaces of peatlands, leading to microtopographic, hydrological and vegetation  
60 gradients within a single site [1].

61  
62 Tropical peatlands are thought to contain approximately 88.6 Gt of carbon, equivalent to 15-19 %  
63 of the global peatland carbon pool [4, 5]. They support important ecosystems and are found in both  
64 lowland and upland areas in SE Asia, Africa and Central and South America [6, 7, 8, 9]. A wide va-  
65 riety of peatlands have recently been discovered in the subsiding Pastaza-Marañón basin in Peruvian  
66 Amazonia including minerotrophic palm swamps (peatlands that receive surface runoff and/or ground-  
67 water recharge from surrounding mineral-soil sources) and ombrotrophic domed bogs (peatlands that  
68 receive all water and nutrients from direct precipitation). These peatlands have been classified by  
69 differences in surface nutrient status, topography and vegetation communities [8, 10]. Peat thickness  
70 is also variable (from <1 to 7.5 m) [8, 10]. These peatlands are different to those in SE Asia as they  
71 have not been heavily disturbed by human activity and the domed bogs may therefore be the best  
72 remaining examples in the world [10, 11]. Peatlands have also been recently reported from Central  
73 Amazonia (Brazil), although peat thicknesses are not as great as in the west [12].

74  
75 Peatlands in the tropics are vulnerable to destabilisation through climate-induced changes and hu-  
76 man activities including deforestation, drainage and burning [5, 13, 14]. To fully understand how  
77 tropical peatlands may respond to such drivers of change, knowledge of their developmental history  
78 and past ecohydrological dynamics is needed. Testate amoebae (Protozoa: Rhizopoda) are a poly-  
79 phyletic group of protozoans characterised by morphologically distinct tests [15]. Testate amoebae are  
80 often found in abundance living on the surface of peatlands (comprising up to 30% of the microbial

81 biomass) and subfossil remains are often preserved in peats [15, 16]. The use of testate amoebae for  
82 palaeohydrological reconstruction is well established for mid-latitude peatlands [16, 17, 18, 19, 20, 21]  
83 and subarctic/boreal peatlands to a lesser extent [22]. Palaeohydrological reconstruction in peatlands  
84 is achieved using calibration models known as transfer functions which are based on the modern rela-  
85 tionship between taxa and the environmental variable(s) of interest [16, 19]. The potential of testate  
86 amoebae as hydrological indicators in tropical peatlands has not yet been assessed despite several  
87 ecological studies of testate amoebae in the tropics [23, 24, 25]. Hydrological reconstructions from  
88 tropical peatlands may prove particularly useful as relatively little hydrological monitoring data exists,  
89 especially from sites in Africa and S. America.

90

91 This paper has three aims:

- 92 (1) To describe the testate amoebae communities in an Amazonian peatland;
- 93 (2) To determine the most important environmental parameters that influence the testate amoeba  
94 communities. We test the hypothesis that water table depth is the strongest environmental control on  
95 the distribution of testate amoebae in an Amazonian peatland;
- 96 (3) To elucidate whether testate amoeba transfer functions for the reconstruction of hydrological change  
97 can be developed in these environments.

98

## 99 **2 Study site**

100 Aucayacu is a nutrient-poor domed peatland in Peruvian Amazonia which now operates as an om-  
101 brotrophic 'raised bog' system [10]. It is situated on alluvial fan sediments between a stream of the  
102 Pastaza fan and the Tigre River (Figure 1). The peatland was initially a nutrient rich minerotrophic  
103 system that gradually became an ombrotrophic raised bog [11]. Aucayacu represents the deepest peat-  
104 land that has been discovered in the Amazon basin (up to 7.5 m thick) and peat initiation at the site  
105 has been dated to c. 8870 cal. BP [11]. The vegetation of Aucayacu is characterised by 'pole' and  
106 'dwarf' forest communities.

107

108 At the nearby city of Iquitos (Figure 1), average annual rainfall of up to 3000 mm is typical, with  
109 the wet season spanning the months November to March when the Inter Tropical Convergence Zone

110 (ITCZ) has migrated just south of the equator and is positioned over northern Peru [26]. Even the dry  
111 season from June to September can experience monthly rainfall totals of up to 170 mm [27]. Owing  
112 to its equatorial position, the altitude of the midday sun is always close to vertical, leading to nearly  
113 constant monthly temperatures throughout the year. The average annual temperature at Iquitos is  
114 26°C, with a diurnal range of approximately 10°C (30-32°C daytime temperatures and 21-22°C at  
115 night) [27]. The climate of this region is classed as equatorial under the Köppen climate classification  
116 (*Af*).

### 117 **3 Methods**

118 A 1.4 km-long linear transect from the edge to the interior of the Aucayacu peatland was estab-  
119 lished and 100 surface sampling points were specifically selected to cover the entire microtopographi-  
120 cal/hydrological gradient. A slight change in direction was needed half-way along the transect to avoid  
121 working in an area containing snakes. The transect was surveyed using a Leica level and staff and the  
122 locations of the sample points recorded using a hand-held GPS. Litter samples of approximately 5 cm<sup>3</sup>  
123 were sampled from each point and placed into ziplock bags. The size and shape of each microform  
124 along with the vegetation composition (within an area of 5 m<sup>2</sup>), % litter and vegetation cover were  
125 recorded at each location (Supplementary file 1, 2). A hole was augered at each sampling point and  
126 the water table depth measured at regular intervals until it equalised before being measured with a  
127 metal ruler (Supplementary file 3). The water table measurements were carried out over a three day  
128 period to ensure they were internally consistent. pH and conductivity measurements were carried out  
129 on water samples extracted from the boreholes using calibrated field meters. One core, 0-1m depth,  
130 was extracted from the interior of the Aucayacu peatland using a Russian corer following the parallel  
131 hole method [28, 29].

132  
133 Following courier transport, all samples were returned to the laboratory and stored in refrigeration at  
134 4°C prior to further analysis. Approximately one half of each litter sample was weighed, oven dried and  
135 re-weighed to determine moisture content. The samples were subsequently burnt in a muffle furnace at  
136 450°C for 8 hours to determine loss-on-ignition [30]. Testate amoebae were prepared using a modified  
137 version of the standard method [31]. Samples of known volume were sieved through a 300 µm sieve  
138 and no fine-sieving was carried out following [32]. The samples were stored in deionised water. Testate

139 amoebae were counted under transmitted light at 200-400 $\times$  and identified using morphology, compo-  
140 sition, size and colour to distinguish taxa. At least 100 specimens were counted per sample [33]. The  
141 taxonomy uses a morphospecies approach in certain circumstances, where a designation that includes  
142 other species has been classed as a "type". Testate amoebae were identified using several standard keys  
143 [34, 35, 36, 37, 38]. Scanning electron microscope images were taken using a Hitachi S-3700N scanning  
144 electron microscope (<http://www.sem-eds.amu.edu.pl/>). The peat core for the palaeoenvironmental  
145 study was sub-sampled in the laboratory and samples were prepared for testate amoebae analysis as  
146 outlined above.

147  
148 Above ground plant material (e.g. leaf fragments, wood and seeds) were extracted from the peat  
149 samples and AMS  $^{14}\text{C}$  dates at  $^{14}\text{Chrono}$  (Queen's University Belfast) and the SUERC Accelerator  
150 Mass Spectrometer Laboratory (East Kilbride, Scotland). All samples were acid-alkali-acid washed  
151 prior to analysis. We looked for Spheroidal Carbonaceous Particles (SCPs) in the top 50 cm of the  
152 peat core in an attempt to date the recent century [39]; however, none were present.

153  
154 The gradient length of the contemporary data was determined using Detrended Correspondence Analy-  
155 sis (DCA). As the data are characterised by a long gradient, Canonical Correspondence Analysis (CCA)  
156 was used to explore the relationships between testate amoebae taxa and environmental variables. The  
157 relative contributions of the environmental variables were investigated using a series of partial CCAs  
158 [40], enabling an estimation of how the total variance is partitioned and the intercorrelations between  
159 variables. Monte-Carlo permutation tests were used to determine the statistical significance of these  
160 analyses (e.g. Dale and Dale 2002). Our use of CCA enables direct comparisons with previous studies  
161 of peatland testate amoebae that have relied on this technique. A number of environmental variables  
162 (plant functional types, distances and heights, peat thickness, % litter and vegetation cover, number  
163 of plant taxa, microform area) were considered as indirect factors and were included as passive (sup-  
164plementary) variables in the analysis. As there have been some criticisms of the use of the  $\chi^2$  distance  
165 in CCA [42, 43], Nonmetric Multidimensional Scaling (NMDS), [44, 45] was also used to examine the  
166 relationship between testate amoebae and environmental variables. In contrast to CCA, NMDS does  
167 not make assumptions about species distributions over environmental gradients. Species data were  
168 square root transformed prior to NMDS ordination and Sorensen distance measure was used. The

169 optimum solution was identified through comparison of final stress values. The analysis was carried  
170 out using the Vegan package in R version 2.15.1 [46, 47]. The Shannon Diversity Index (SDI) was used  
171 to examine the community diversity [48]. The SDI is defined as:

172

173

174

$$SDI = \sum_{i=1}^s \left( \frac{X_i}{N_i} \right) \ln \left( \frac{X_i}{N_i} \right)$$

175

176

177 where  $X_i$  is the abundance of each taxon in a sample,  $N_i$  is the total abundance of the sample,  
178 and  $s$  is equal to the species richness of the sample. Environments are considered to be healthy if  
179 the SDI falls between 2.5 and 3.5, in transition between 1.5 and 2.5, and stressed between 0.1 and 1.5  
180 [49, 50].

181

182 Detrended Canonical Correspondence Analysis (DCCA) was performed on the dataset to determine  
183 the gradient length and therefore to deduce whether linear or unimodal-based regression methods  
184 would best represent the taxon-environment relationships [51]. Transfer functions were constructed  
185 using several regression models - Weighted averaging (WA), tolerance-downweighted weighted averag-  
186 ing (WA-Tol), locally-weighted weighted averaging (LWWA), weighted averaging partial least-squares  
187 (WA-PLS) and maximum likelihood (ML). Models were also developed using the modern analogue  
188 technique (MAT) and weighted modern analogue technique (WMAT). The models were built using C2  
189 [52]. The performance of the models was assessed using  $r^2$  and the root mean square error of prediction  
190 (RMSEP) with leave-one-out cross validation (jack-knifing) and bootstrapping. The transfer function  
191 models were improved through removal of 19 samples with high residual values ( $>10$  cm). A further 11  
192 samples were screened out based on influence of other (non-hydrological) factors. The best performing  
193 model was the one based on WA-PLS (component 2). This water table transfer function was applied to  
194 subfossil data and sample-specific errors of prediction were generated by 999 bootstrap cycles [53, 54].

## 195 4 Results

### 196 4.1 Site characteristics

197  
198 The topographic survey illustrates that Aucayacu is a domed peatland with a steep rand (Figure  
199 2). Environmental parameters vary within the peatland and there is clear evidence of river influence  
200 at the edge of the site causing higher pH and reduced loss-on-ignition (through delivery of minerogenic  
201 material). A silty clay deposit underlies the peatland and there is a small natural levee at the peatland  
202 edge (Figure 2). The vegetation survey suggests the presence of at least 87 plant taxa (Figure 3;  
203 Supplementary file 1), the most commonly encountered trees and 'small trees' include *Alibertia* sp. 1,  
204 *Iryanthera ulei*, *Virola pavonis*, *Zygia* sp. 1 and *Oxandra euneura*. The most commonly occurring palm  
205 trees are *Mauritia flexuosa* and *Oenocarpus mapora*. Understory herbs include *Trichomanes pinnatum*  
206 and *Pariana* sp. 1. There are variations in the distribution of plant functional types (PFTs) and the  
207 relative contribution of different plant families across the site (Figure 3). For example, individuals from  
208 the families Myristicaceae and Arecaceae become more abundant with distance from the river. Plants  
209 from the Euphorbiaceae and Annonaceae families are well represented in both the peatland margins  
210 and interior, whereas there is a zone dominated by plants of the Rubiaceae family approximately 500-  
211 800 m from the river.

212  
213 A series of microforms (ecohydrologically distinct surface features within the mire microtope [55])  
214 was encountered in the Aucayacu peatland including hollows and pools the latter characterised by  
215 standing water), flat areas ('litter flats'), raised ridges and mounds of accumulated litter ('litter hum-  
216 mocks' and 'ridges') and raised areas caused by litter accumulation around the roots of large trees  
217 ('tree hummocks'). Photos of these microforms are provided in Supplementary file 2. These micro-  
218 forms range in scale from <1 to 20 m<sup>2</sup>. The pools and hollows become larger in the interior of the  
219 peatland and more aligned to the contours, similar to Northern peatlands (Figure 2, Supplementary  
220 file 2). The microforms are characterised by contrasting water table depths (Figure 4, Supplementary  
221 file 3).

### 223 4.2 Ecology of testate amoebae

224

225 A total of 47 testate amoebae taxa from 21 genera were identified at Aucayacu (Figures 5, 6ab,  
226 Table 1). The most common taxa are *Cryptodiffugia oviformis*, *Euglypha rotunda* type, *Phryganella*  
227 *acropodia*, *Pseudodiffugia fulva* type and *Trinema lineare*. One species found only in the southern  
228 hemisphere, *Argygnia spicata*, is present [56]. *Arcella* spp., *Centropyxis aculeata* and *Lesqueresia spi-*  
229 *ralis* are indicators of pools with standing water. We recorded one potentially new species of *Arcella* -  
230 details of which will be published elsewhere. The Shannon Diversity Index values of the samples range  
231 between 0.8-2.8.

232  
233 CCA axes one (eigenvalue = 0.149) and two (eigenvalue = 0.063) explain 11.7% of the variance in  
234 the testate amoebae data (Figure 7). The hydrological variables (moisture content and water table)  
235 and loss-on-ignition are strongly correlated to axis one. The associated Monte Carlo permutation test  
236 shows that CCA axis one is highly significant ( $p < 0.001$ , 999 random permutations), pH and conductiv-  
237 ity are correlated with axis two. A series of partial CCAs show that water table depth explains 15.3%  
238 of the variance in the data ( $p < 0.002$ ). pH explains 12.9% ( $p < 0.002$ ), Moisture content explains 8.9%  
239 ( $p < 0.025$ ), conductivity explains 11.8% ( $p < 0.030$ ) and loss-on-ignition explains 10.0% ( $p < 0.0470$ ).  
240 The strong influence of hydrological variables is also illustrated by the NMDS ordination as water  
241 table and moisture content are correlated with NMDS coordinate 1 (Figure 7).

242

#### 243 4.3 Transfer function and application to core

244

245 The performance statistics for the transfer function models are shown in Table 2. The best perform-  
246 ing transfer function model (Figure 8) is based on weighted averaging partial least-squares (WAPLS)  
247 component 2 ( $r^2_{\text{apparent}} = 0.53$ , RMSE = 7.70,  $r^2_{\text{jack}} = 0.40$ , RMSEP = 9.13). After the screening  
248 of samples (Supplementary file 5) the model performance greatly improved ( $r^2_{\text{apparent}} = 0.76$ , RMSE  
249 = 4.29;  $r^2_{\text{jack}} = 0.68$ , RMSEP = 5.18). The most common subfossil testate amoebae present in the  
250 core from Aucayacu include *Hyalosphenia subflava* "major" ( $> 60\mu\text{m}$ ), *Hyalosphenia subflava* "minor"  
251 ( $< 60\mu\text{m}$ ), *Phryganella acropodia*, *Trigonopyxis arcuata* "polygon aperture", *Centropyxis aculeata* and  
252 *Cryptodiffugia oviformis*. A count of over 100 specimens was achieved for all the core samples and  
253 tests were generally well-preserved. However, concentrations were very low and the analysis of several  
254 samples took many hours. The transfer function was applied to the subfossil data and there were no

255 missing modern analogues. The directional changes in the water table reconstruction are mirrored  
256 by principal NMDS axis one scores, suggesting that the transfer function is correctly representing the  
257 structure in the subfossil data (Supplementary file 6). The reconstruction suggests near-surface water  
258 tables over the last 3,000 years (Figure 9; Supplementary file 7) with a marked shift to drier conditions  
259 at c. 50 cm (c. cal. AD 1218-1273).

## 260 **5 Discussion**

261 To our knowledge this is the first study examining the ecology of testate amoebae in a tropical peatland.  
262 We have demonstrated that testate amoebae are sensitive hydrological indicators in this Amazonian  
263 peatland, suggesting they have the potential to be used more widely in Amazonia and perhaps in the  
264 tropics more widely. The multivariate statistical analysis illustrates the strong hydrological controls on  
265 the distribution of testate amoebae, similar to the research findings from mid- and high latitude peat-  
266 lands [16, 17, 18, 19, 20, 21, 22]. pCCA also shows that pH is an important control on testate amoebae  
267 in the Aucayacu peatland - two species (*Trinema grandis*, *Pyxidicula operculata*) are indicators of  
268 higher pH conditions. However, the statistical analysis also demonstrates that a large proportion of  
269 variance in the testate amoeba data remains unexplained. This may be due to a combination of inter-  
270 correlations between environmental variables and unmeasured environmental (edaphic/abiotic) factors.  
271 Such factors may include the characteristics of the canopy (determining the amount of moisture reach-  
272 ing the peatland surface), litter quality, diversity and decomposition [25], variations in nutrient status,  
273 and other unmeasured geochemical factors. It has also been suggested that short-term environmental  
274 variability may be an important factor in the community dynamics of testate amoebae [57]. There is  
275 evidence that the Aucayacu stream has an influence on the SW margin of the peatland (increased pH  
276 and decreased loss-on-ignition - Figure 2) which may affect the testate amoebae communities there.  
277 There is also a possibility that occasional high-magnitude river flooding events affect the peatland  
278 interior, although there is no evidence for this.

279  
280 There appear to be differences in the ecology of certain species compared to the findings from mid- and  
281 high latitude peatlands. For example, *Hyalosphenia subflava*, *Diffflugia pulex* and *Trigonopyxis arcula*  
282 are not unambiguous dry indicators as reported from mid-latitude *Sphagnum* peatlands [19, 21, 58].  
283 However, the ecology of these taxa may be complex since in more recent studies they have also been

284 observed in wet fen environments as well as dry bog hummocks in subarctic and boreal peatlands [22].  
285 The large abundance of *Diffflugia pulex* and *Hyalosphenia subflava* in this tropical peatland is par-  
286 ticularly interesting as there have been some problems finding modern analogues for these taxa in  
287 temperate peatlands [16, 18, 15] and it has also been suggested that these two taxa are characteristic  
288 of highly variable conditions [57]. However, *Centropyxis aculeata* is consistently a wet indicator in  
289 our study and temperate peatlands [59]. There is morphological variability of certain taxa reported  
290 here such as the marked differences in the aperture of *Trigonopyxis arcuata*. Ogden and Hedley (1980)  
291 describe the highly variable aperture shape of *T. arcuata* [35], which was also noted by Bobrov et al.  
292 (1995) in populations from Russia and Canada including the occurrence of 3-point, 4-point and almost  
293 polygonal/circular apertures [60].

294  
295 Palaeohydrological reconstructions based on testate amoebae may prove particularly useful for exam-  
296 ining the developmental history of tropical peatlands. Previous pollen and stratigraphic data suggest  
297 that Amazonian peatlands undergo major vegetation transitions in their developmental history [61].  
298 Testate amoebae may provide important information about the role of changing hydrology across such  
299 ecological transitions. However, poor preservation of tests may hinder this for older sections of the  
300 subfossil record [62, 63, 64].

301  
302 Relatively little is currently known about the ecohydrological dynamics of tropical peatlands. Peatland  
303 development models [65, 66] modified for tropical ecosystem PFTs, productivity and decomposition  
304 (e.g. [67]) may shed light on the long-term ecohydrological and C dynamics of these systems. Of  
305 particular interest is how peatlands respond to climatic shifts [68]. Testate amoebae-based reconstruc-  
306 tions may therefore prove useful for testing the hydrological outputs of such models and understanding  
307 peatland responses to changing climate. In the case of Amazonian peatlands, changing flooding regime  
308 through time and river channel migration may also affect the peatland development trajectories [11].

309  
310 Previous palaeoenvironmental studies of lakes and swamps in Amazonia have suggested distinct phases  
311 of climate changes during the Holocene. For example, there is compelling evidence for a period of in-  
312 creased precipitation from several areas of Amazonia at c. 700-1300 cal. BP [69, 70, 71, 72, 73].  
313 Peatlands have the potential to provide high resolution archives of environmental and climatic change

314 during this period and could add substantial temporal and spatial detail to the existing picture. Fur-  
315 ther work is needed to identify a clear climatic signal in the Amazonian peatland archives as their  
316 accumulation is controlled by a complex interaction of biological, geochemical, hydrological and cli-  
317 matic factors. Future studies should focus on i) the generation of modern and palaeoecological data  
318 from other suitable sites; ii) the development of robust core chronologies; iii) high-resolution sampling;  
319 iv) multiproxy approaches; v) inter and intra-site comparison studies and vi) the comparison of peat-  
320 based reconstructions to independent palaeoclimatic data. Furthermore, hydrological monitoring data  
321 will help understand the sub-annual and inter-annual hydrological dynamics of Amazonian peatlands.

322  
323 There are major concerns about the effects of climate change and human activity on tropical peatlands  
324 as they are globally important carbon sinks [4, 5]. Future climate change scenarios for north-east Peru,  
325 derived from an average of 21 climate models and expressed as relative changes from the 1961-1990  
326 baseline climate to the year 2100, project an average annual increase in temperatures of  $3.0 - 3.5^{\circ}\text{C}$   
327 and a 5 – 10% increase in precipitation across the region [27]. Agreement between models is generally  
328 low (particularly for precipitation), but nonetheless a consistent pattern of warming and increasing  
329 precipitation is projected [27]. As the Amazonian basin is of special interest as a biodiversity hotspot  
330 [74], further research is needed to examine the sensitivity of Amazonian peatlands to climate change  
331 and loss of biodiversity from human impacts. Our study suggests that testate amoebae may prove to be  
332 a particularly useful tool in this endeavour by enabling us to reconstruct past hydrological conditions  
333 which are crucial to the functioning of these ecosystems.

334

## 335 6 Conclusions

336 (1) We present the first analysis of testate amoebae from a tropical peatland (Aucayacu, Peruvian  
337 Amazonia). We recorded 47 testate amoebae taxa from 21 genera in surface litter samples. The most  
338 common taxa are *Cryptodiffugia oviformis*, *Euglypha rotunda* type, *Phryganella acropodia*, *Pseudodif-*  
339 *flugia fulva* type and *Trinema lineare*. *Arcella* spp., *Centropyxis aculeata* and *Lesqueresia spiralis* are  
340 indicators of pools with standing water.

341

342 (2) Multivariate statistical analysis illustrates that water table depth is the most important control

343 on the distribution of testate amoebae in the peatland explaining 15.3% of the variance in the data  
344 ( $p < 0.002$ ). pH is the next most important variable explaining 12.9% ( $p < 0.002$ ). A transfer function  
345 model for water table based on weighted averaging partial least-squares (WAPLS) regression is pre-  
346 sented and performs well under cross validation ( $r_{\text{apparent}}^2 = 0.76$ , RMSE = 4.29;  $r_{\text{jack}}^2 = 0.68$ , RMSEP  
347 = 5.18).

348  
349 (3) The transfer function was applied to a 1-m peat core and sample-specific reconstruction errors  
350 were generated using bootstrapping. The reconstruction generally suggests near-surface water tables  
351 over the last 3,000 years, with a marked shift to drier conditions at c. cal. AD 1218-1273. Testate  
352 amoebae may prove very useful for reconstructing the hydrological dynamics of tropical peatlands in  
353 Amazonia and elsewhere.

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361 in The Scanning Microscopy and Microanalysis Laboratory, Faculty of Geographical and Geological  
362 Sciences, Adam Mickiewicz University. We kindly thank Monika Lutynska for technical support.

## 363 8 Figure captions

364 Figure 1. Map showing the location of the Aucayacu peatland, Loreto region, Peruvian Amazonia.  
365 Location of the study site is shown on a Landsat TM RGB false color image (NASA Landsat Program,  
366 Orthorectified, WRS-2, Path 007, Row 063, downloaded from <http://earthexplorer.usgs.gov/>). Band  
367 4 was assigned to red, band 5 was assigned to green and band 7 was assigned to blue.

368  
369 Figure 2. Topographic and stratigraphic profile of the Aucayacu peatland with environmental variables

370 measured along the transects.

371

372 Figure 3. Plant families and plant functional types in the Aucayacu peatland (abundance plotted  
373 against distance from the river).

374

375 Figure 4. Boxplot of water table depths measured for each microform type.

376

377 Figure 5. Contemporary percentage testate amoebae data from Aucayacu peatland, ranked in or-  
378 der of water table depth. The total count and Shannon Diversity Index are also shown.

379

380 Figure 6a. Light microscope images of testate amoebae from Aucayacu: A. *Sphenoderia fissirostris*;  
381 B. *Centropyxis aerophila*; C. *Nebela penardiana*; D. *Lesqueresia spiralis*; E. *Cryptodiffugia oviformis*;  
382 F. *Diffflugia pulex*; G. *Tracheleuglypha dentata*; H. *Centropyxis aculeata*; I. *Physochila griseola*; J.  
383 *Quadrullella symmetrica*; K. *Trigonopyxis arcuata* "3-point aperture"; L. *Centropyxis ecornis*.

384

385 Figure 6b. SEM images of testate amoebae from Aucayacu: A. *Argygnnia spicata*; B. *Hyalosphenia*  
386 *subflava* "major" ( $> 60\mu m$ ); C. *Euglypha rotunda* type; D. Aperture of *Euglypha rotunda* type; E.  
387 *Nebela barbata*; F. *Trinema lineare*; G. *Tracheleuglypha dentata*; H. *Physochila griseola*.

388

389 Figure 7. (a) CCA of testate amoebae from Aucayacu and environmental variables (water table  
390 depth, moisture content, pH, conductivity and loss-on-ignition. Abbreviated species codes and sample  
391 numbers are shown (see Table 1). (b) CCA showing environmental variables and other factors plotted  
392 as supplementary variables (plant functional types, number of plant taxa - S, % litter and vegetation,  
393 depth of peatland, distance from river, height above water level, microform area). (c) NMDS ordina-  
394 tion of the species and environmental data.

395

396 Figure 8. Graph of observed versus model estimated water table depth for (a) complete dataset;  
397 (b) screened dataset.

398

399 Figure 9. Subfossil testate amoebae diagram from Aucayacu (data are expressed as percentages).

400 The water table reconstruction and Shannon Diversity Index values are shown. Radiocarbon dates are  
401 illustrated.

402

403 Table 1. Taxon codes.

404

405 Table 2. Transfer function model performance statistics.

406

407 Supplementary file 1. Vegetation survey data from Aucayacu.

408

409 Supplementary file 2. Photographs of peatland microforms at Aucayacu.

410

411 Supplementary file 3. Water table equalisation graphs.

412

413 Supplementary file 4. CCA results.

414

415 Supplementary file 5. Samples removed from the refined transfer function.

416

417 Supplementary file 6. Aucayacu water table reconstruction compared to NMDS axis 1 scores.

418

419 Supplementary file 7.  $^{14}\text{C}$  dates.

## 420 **References**

- 421 [1] Charman DJ (2002) Peatlands and Environmental Change. Wiley-Blackwell.
- 422 [2] Holden J (2005) Peatland hydrology and carbon release: Why small-scale process matters. Philo-  
423 sophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences  
424 363: 2891-2913.
- 425 [3] Belyea LR, Baird AJ (2006) Beyond the limits to peat bog growth: cross-scale feedback in peatland  
426 development. Ecological Monographs 76: 299-322.
- 427 [4] Page SE, Rieley JO, Banks BG (2008) Global and regional importance of the tropical peatland  
428 carbon pool. Global Change Biology 17: 798-818.
- 429 [5] Moore S, Evans CD, Page SE, Garnett MH, Jones T, Freeman C, Hooijer A, Wiltshire AJ, Limin  
430 SH, Gauci V (2013) Deep instability of deforested tropical peatlands revealed by fluvial organic  
431 carbon fluxes. Nature 493: 660-663.
- 432 [6] Anderson JAR (1964) The structure and development of the peat swamps of Sarawak and Brunei.  
433 The Journal of Tropical Geography 18: 716.
- 434 [7] Joosten H (2009) The Global Peatland CO<sub>2</sub> Picture. Wetlands International, Ede: 33 pp.
- 435 [8] Lahteenoja O, Ruokolainen K, Schulman L, Alvarez J (2009a) Amazonian floodplains harbour  
436 minerotrophic and ombrotrophic peatlands. Catena 79: 140-145.
- 437 [9] Lahteenoja O, Ruokolainen K, Schulman L, Oinonen M (2009b) Amazonian peatlands: an ignored  
438 C sink and potential source, Global Change Biology 15: 2311-2320.
- 439 [10] Lahteenoja O, Page SE (2011) High diversity of tropical peatland ecosystem types in the Pastaza-  
440 Maraon basin, Peruvian Amazonia. Journal of Geophysical Research 116: G02025.
- 441 [11] Lahteenoja O, Reategui Y, Rasanen M, del Castillo D, Oinonen M, Page SE (2012) The large  
442 Amazonian peatland carbon sink in the subsiding astaza-Maraon foreland basin, Peru. Global  
443 Change Biology 18: 1641-1678.
- 444 [12] Lahteenoja O, Flores B, Nelson B (2013) Tropical peat accumulation in Central Amazonia. Wet-  
445 lands 33: 495-503.

- 446 [13] Page SE, Siegert F, Rieley JO, Boehm HDV, Jaya A, Limin S (2002) The amount of carbon  
447 released from peat and forest fires in Indonesia in 1997. *Nature* 420: 61-65.
- 448 [14] Miettinen J, Shi C, Liew SC (2012) Two decades of destruction in Southeast Asia's peat swamp  
449 forests. *Frontiers in Ecology and the Environment* 10: 124128.
- 450 [15] Mitchell EAD, Charman DJ, Warner BG (2008) Testate amoebae analysis in ecological and paleo-  
451 oecological studies of wetlands: past, present and future. *Biodiversity and Conservation* 17: 2115-  
452 2137.
- 453 [16] Woodland WA, Charman DJ, Sims PC (1998) Quantitative estimates of water tables and soil  
454 moisture in Holocene peatlands from testate amoebae. *The Holocene* 8: 261273.
- 455 [17] Lamentowicz M, Mitchell EAD (2005) The ecology of testate amoebae (Protists) in sphagnum in  
456 North-western Poland in relation to peatland ecology. *Microbial Ecology* 50, 1: 48-63.
- 457 [18] Charman DJ, Blundell A, ACCROTELM Members (2007) A new European testate amoebae  
458 transfer function for palaeohydrological reconstruction on ombrotrophic peatlands. *Journal of Qua-*  
459 *ternary Science* 22: 209221.
- 460 [19] Swindles GT, Charman DJ, Roe HM, Sansum PA (2009) Environmental controls on peatland  
461 testate amoebae (Protozoa: Rhizopoda) in the North of Ireland: Implications for Holocene palaeo-  
462 climate studies. *Journal of Paleolimnology* 42: 123-140.
- 463 [20] Turner TE., Swindles GT, Charman DJ, Blundell A (2013) Comparing regional and supra-regional  
464 transfer functions for palaeohydrological reconstruction from Holocene peatlands. *Palaeogeography,*  
465 *Palaeoclimatology, Palaeoecology* 369: 395408.
- 466 [21] Amesbury MJ, Mallon G, Charman DJ, Hughes PD, Booth RK, Daley TJ, Garneau M (2013)  
467 Statistical testing of a new testate amoebae transfer function for water-table depth reconstruction  
468 on ombrotrophic peatlands in Atlantic Canada and far north-eastern United States. *Journal of*  
469 *Quaternary Science* 28: 27-39.
- 470 [22] Lamarre A, Magnan G, Garneau M, Boucher E (In Press) A testate amoeba-based transfer  
471 function for paleohydrological reconstruction from boreal and subarctic peatlands in northeast-  
472 ern Canada. *Quaternary International*.

- 473 [23] Bobrov AA (2001) Findings of the Tropical Group Testate Amoebae (Protozoa: Testacea) at the  
474 Far East (Sikhote Alin Reserve). *Biology Bulletin of the Russian Academy of Sciences* 28: 401-407.
- 475 [24] Krashevskaya V, Bonkowski M, Maraun M, Scheu S (2007) Testate amoebae (protista) of an eleva-  
476 tional gradient in the tropical mountain rain forest of Ecuador. *Pedobiologia* 51: 319331.
- 477 [25] Krashevskaya V, Maraun M, Scheu S (2012) How does litter quality affect the community of soil pro-  
478 tists (testate amoebae) of tropical montane rainforests? *FEMS Microbiology Ecology* 80: 603607.
- 479 [26] Martinez R, Ruiz D, Andrade M, Blacutt L, Pabon D, Jaimes E, Leon G, Villacis M, Quintana J,  
480 Montealegre E, Euscategui CH (2011) Synthesis of the climate of the Tropical Andes. Pages 97-109  
481 in Herzog SK, Martinez R, Jorgensen, PM, Tiessen H (eds.). *Climate change and biodiversity in*  
482 *the Tropical Andes*. MacArthur Foundation, Inter-American Institute of Global Change Research  
483 (IAI) and Scientific Committee on Problems of the Environment (SCOPE), Sao Jose dos Campos  
484 and Paris, 348 pp., ISBN: 978-85-99875-05-6.
- 485 [27] Met Office (2011) *Climate: Observations, Projections and Impacts*. Peru. Met Office: Exeter.
- 486 [28] Jowsey PC (1966) An improved peat sampler. *New Phytologist* 65: 245248.
- 487 [29] De Vleeschouwer F, Chambers FM, Swindles GT (2010) Coring and sub-sampling of peatlands  
488 for palaeoenvironmental research. *Mires and Peat* 7: 1-10.
- 489 [30] Schulte EE, Hopkins BG (1996) Estimation of soil organic matter by weight-loss-on-ignition. In  
490 FR Magdoff et al. (eds) *Soil organic matter: analysis and interpretation*. SSSA Spec. Publ. 46,  
491 Madison, WI.
- 492 [31] Hendon D, Charman DJ (1997) The preparation of testate amoebae (Protozoa: Rhizopoda) sam-  
493 ples from peat. *The Holocene* 7: 199-205.
- 494 [32] Payne R (2009) The standard preparation method for testate amoebae leads to selective loss of  
495 the smallest shells. *Quaternary Newsletter* 119: 16-20.
- 496 [33] Payne R, Mitchell E (2009) How many is enough? Determining optimal count totals for ecological  
497 and palaeoecological studies of testate amoebae. *Journal of Paleolimnology* 42: 483-495.
- 498 [34] Charman DJ, Hendon D, Woodland W (2000) The identification of peatland testate amoebae.  
499 *Quaternary Research Association Technical Guide* 9: 147pp.

- 500 [35] Ogden CG, Hedley RH eds. (1980) An Atlas to Freshwater Testate Amoebae, London: Oxford  
501 University Press.
- 502 [36] Mazei Y, Tsyganov AN (2006) Freshwater Testate Amoebae. Moscow, KMK.
- 503 [37] Meisterfeld R (2000) Arcellinida. The Illustrated Guide to the Protozoa, Second Edition: 827-859.
- 504 [38] Meisterfeld R (2000) Testate Amoebae with Filopodia. The illustrated Guide to the Protozoa,  
505 Second Edition: 1054-1083.
- 506 [39] Swindles GT (2010) Dating recent peat profiles using spheroidal carbonaceous particles (SCPs).  
507 Mires and Peat 7: 1-10.
- 508 [40] Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological  
509 variation. Ecology 73: 1045-1055.
- 510 [41] Dale B, Dale AL (2002) Application of ecologically based statistical treatments to micropalaeon-  
511 tology. In: Haslett SK (ed) Quaternary environmental micropalaeontology. Arnold, London.
- 512 [42] Rao CR (1995) A review of canonical coordinates and an alternative to correspondence analysis  
513 using Hellinger distance. Qüestiió 19: 2363.
- 514 [43] Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species  
515 data. Oecologia 129: 271-280.
- 516 [44] Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:  
517 115-129.
- 518 [45] McCune B, Grace JB (2002) Analysis of Ecological Communities. MJM Press.
- 519 [46] Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos  
520 P, Henry M, Stevens H, Wagner H (2012) vegan: Community Ecology Package. [http://CRAN.R-](http://CRAN.R-project.org/package=vegan)  
521 [project.org/package=vegan](http://CRAN.R-project.org/package=vegan)
- 522 [47] R Core Team (2012). R: A language and environment for statistical computing. R Foundation for  
523 Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- 524 [48] Shannon CE (1948) A mathematical theory of communication. The Bell System Technical Journal  
525 27: 379-423 and 623-656.

- 526 [49] Magurran AE (1988) Ecological Diversity and Its Measurement. Princeton: Princeton University  
527 Press.
- 528 [50] Patterson RT, Kumar A (2000) Assessment of arcellacea (thecamoebian) assemblages, species and  
529 strains as contaminant indicators in variably contaminated James Lake, north Eastern Ontario.  
530 Journal of Foraminiferal Research 30: 310-320.
- 531 [51] Birks HJB (1995) Quantitative palaeoenvironmental reconstructions. In: Maddy D, Brew JS  
532 (eds) Statistical Modelling of Quaternary Science Data. Technical guide 5. Quaternary Research  
533 Association, Cambridge.
- 534 [52] Juggins S (2003) C2 user guide. Software for ecological and palaeoecological data analysis and  
535 visualisation. University of Newcastle, Newcastle Upon Tyne.
- 536 [53] Birks HJB, Line JM, Juggins S, Stevenson AC, ter Braak CJF (1990) Diatoms and pH recon-  
537 struction. Philosophical Transactions of the Royal Society B 27: 263278.
- 538 [54] Line JM, ter Braak CJF, Birks HJB (1994) WACALIB version 3.3: a computer program to  
539 reconstruct environmental variables from fossil assemblages by weighted-averaging and to derive  
540 sample-specific errors of prediction. Journal of Paleolimnology 10: 147152.
- 541 [55] Ivanov KE (1981) Water Movement in Mirelands. Academic Press, London.
- 542 [56] Deflandre G (1936) Etude monographique sur le genre Nebela Leidy. Annales de Protistologie 5:  
543 201-286.
- 544 [57] Sullivan ME, Booth RK (2011) The potential influence of short-term environmental variability  
545 on the composition of testate amoeba communities in *Sphagnum peatlands*. Microbial Ecology 62:  
546 80-93.
- 547 [58] Turner TE, Swindles GT (2012) Ecology of testate amoebae in moorland with a complex fire  
548 history: implications for ecosystem monitoring and sustainable land management. Protist 163:  
549 844-855.
- 550 [59] Booth RK, Zygmunt JR (2005) Biogeography and comparative ecology of testate amoebae inhab-  
551 iting *Sphagnum*-dominated peatlands in the Great Lakes and Rocky Mountain regions of North  
552 America. Diversity and Distributions 11: 577-590.

- 553 [60] Bobrov AA, Yazvenko SB, Warner BG (1995) Taxonomic and ecological implications of shell  
554 morphology of three testaceans (Protozoa: Rhizopoda) in Russia and Canada. *Archiv für Protis-*  
555 *tenkunde* 145: 119-126.
- 556 [61] Roucoux KH, Lawson IT, Jones TD, Baker TR, Coronado ENH, Gosling WD, Läähteenoja O  
557 (2013) Vegetation development in an Amazonian peatland, *Palaeogeography, Palaeoclimatology,*  
558 *Palaeoecology* 374: 242-255.
- 559 [62] Wilmshurst JM, Wiser SK, Charman DJ (2003) Reconstructing Holocene water tables in New  
560 Zealand using testate amoebae: Differential preservation of tests and implications for the use of  
561 transfer functions. *The Holocene* 13: 61-72.
- 562 [63] Swindles GT, Roe HM (2007) Examining the dissolution characteristics of testate amoebae (Pro-  
563 tozoa: Rhizopoda) in low pH conditions: Implications for peatland palaeoclimate studies. *Palaeo-*  
564 *geography, Palaeoclimatology, Palaeoecology* 252: 486-496.
- 565 [64] Mitchell E, Payne R, Lamentowicz M (2008) Potential implications of differential preservation of  
566 testate amoeba shells for paleoenvironmental reconstruction in peatlands. *Journal of Paleolimnology*  
567 40: 603-618.
- 568 [65] Frohling S, Roulet NT, Tuittila E, Bubier JL, Quillet A, Talbot J, Richard PJH (2010) A new  
569 model of Holocene peatland net primary production, decomposition, water balance, and peat ac-  
570 cumulation. *Earth System Dynamics* 1: 121.
- 571 [66] Morris PJ, Belyea LR, Baird AJ (2011) Ecohydrological feedbacks in peatland development: A  
572 theoretical modelling study. *Journal of Ecology* 99: 1190-1201.
- 573 [67] Kurnianto, S (2013) Modeling carbon accumulation dynamics in tropical peat swamp forests  
574 (abstract), *New Frontiers in Tropical Biology: The Next 50 Years (A Joint Meeting of ATBC and*  
575 *OTS)*.
- 576 [68] Swindles GT, Morris PJ, Baird AJ, Blaauw M, Plunkett G (2012) Ecohydrological feedbacks  
577 confound peat-based climate reconstructions. *Geophysical Research Letters* 39: L11401.
- 578 [69] Bush MB, Colinvaux PA (1988) A 7000-year pollen record from the Amazon lowlands, Ecuador.  
579 *Vegetatio* 76: 141-154.

- 580 [70] Frost I (1988) A Holocene sedimentary record from Anañgucocha in the Ecuadorian Amazon.  
581 Ecology 69: 6673.
- 582 [71] Liu KB, Colinvaux PA (1988) A 5200-year history of Amazon rain forest. Journal of Biogeography  
583 15: 231248.
- 584 [72] Behling H, Berrio J, Hooghiemstra H (1999) Late Quaternary pollen records from the middle  
585 Caquetá river basin in central Columbian Amazon. Palaeogeography, Palaeoclimatology, Palaeoe-  
586 cology 145: 193213.
- 587 [73] Correa-Metrio A, Cabrera KR, Bush MB (2010) Quantifying ecological change through discrimi-  
588 nant analysis: a palaeoecological example from the Peruvian Amazon. Journal of Vegetation Science  
589 21: 695704.
- 590 [74] Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartin I, Sanchez-  
591 Meseguer A, Anderson CL, Figueiredo JP, Jaramillo C, Riff D, Negri FR, Hooghiemstra H, Lund-  
592 berg J, Stadler T, Sarkinen T, Antonelli A (2010) Amazonia through time: Andean uplift, climate  
593 change, landscape evolution, and biodiversity. Science 330: 927-931.