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**Bog microtopography and the climatic sensitivity of testate amoeba communities:
implications for transfer function-based paleo-water table reconstructions**

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1 **Abstract**

2 Although the use of sub-fossil testate amoebae as a proxy for raised bog hydrology in
3 Holocene paleoecological studies is well-established, some detailed aspects of species-
4 environment relationships remain under-researched. One such issue is the effect of bog
5 surface microtopography on the climatic sensitivity of testate amoeba communities. Although
6 it has been suggested that some microforms - especially hummocks - may be less sensitive to
7 climatic forcing than others, this has rarely been objectively tested. To investigate this,
8 subfossil testate amoebae assemblages have been examined in a series of shallow cores
9 collected along a hummock-lawn-hollow transect from a bog in central Ireland and the
10 resulting reconstructed water table records, dated using ^{210}Pb , have been compared with
11 instrumental weather data. Testate amoebae communities in the hollow microform were
12 found to be significantly less diverse than those in the hummock and lawn, and both the
13 hummock and lawn showed statistically significant correlations with instrumental
14 temperature and precipitation data. Therefore, whilst the suggestion that paleoecological
15 investigations should target intermediate bog microforms remains sound, the notion that
16 hummock-based testate amoebae hydrological data are climatically-insensitive is challenged.

17

18 **Key words**

19 Microtopography, raised bogs, paleohydrology, testate amoebae, ^{210}Pb , climate forcing,
20 diversity indices

21

22

23

24 **Introduction**

25 Understanding of the ecology of testate amoebae, a group of shell producing protozoa that
26 inhabit a range of soil, wetland and aquatic habitats, has expanded substantially over recent
27 decades, primarily due to their utility as indicators of past or present ecological conditions
28 [1–19]. The first transfer functions for quantitative reconstruction of bog surface wetness
29 from sub-fossil testate amoebae assemblages (based on empty shells that preserve well in
30 peat and are identifiable to species level) were developed in the 1990s [20–22]. Since then
31 testate amoebae have become an increasingly well-established proxy indicator for peatland
32 paleoecological and environmental-archaeological studies [23–29]. Nevertheless, in spite of
33 our growing understanding of the ecology of testate amoebae and the wide use of these
34 organisms in peatland paleoecology [25, 29, 30], there remain a number of areas which
35 require further investigation, such as the distribution of testate amoebae at fine spatial scales
36 [31, 32] and the competing influences of both short- and long-term environmental variability
37 on testate amoebae composition [33–35]. These issues are of particular relevance to
38 paleoecologists since many studies aim, whether explicitly or implicitly, to take information
39 based on observations of microscopic proxy indicators at a small number of localized
40 sampling locations and ‘up-scale’ those inferences to investigate environmental change at
41 much larger spatial scales [28, 36, 37].

42 The issue of how differences in peatland surface microtopography affect species-environment
43 relationships is another under-researched area. Since the falsification [38, 39] of the ‘cyclic’
44 model of bog growth [40], that posited a largely autogenic natural alternation between
45 hummock and hollow surface microforms as the main driver of peat formation, it has been
46 generally accepted that bog surface wetness is substantially affected by climatic forcing [41].
47 Nevertheless, there remains a suspicion that not all surface microforms are equally responsive
48 to climatic variability, and that hummocks, which have often been shown to be persistent

49 features [39, 42], may be “climatically-complacent” [43]. Although surface microforms have
50 long been known to host distinct testate amoebae communities [6, 18], to date only a few
51 studies have directly investigated variability in response of testate amoebae-environment
52 responses in relation to bog microtopography [34, 44].

53 Whilst previous studies have explored linkages between testate amoebae-derived water table
54 reconstructions (usually expressed as depth to water table – DWT) and instrumental weather
55 data [41, 45, 46], to date there has not yet been an investigation of the effect of bog
56 microtopography on these relationships. This study aims to address this gap and to examine
57 the effect of microtopography on the past climatic sensitivity of testate amoebae. This paper
58 addresses the question of how the relationships between testate amoebae transfer function-
59 derived water table reconstructions and climatic variables differ between microforms, and
60 whether particular microforms contain more sensitive paleoclimate archives than others. This
61 was achieved through the investigation of subfossil testate amoebae assemblages in a series
62 of short cores from an intact raised bog and the comparison of the resulting water table
63 reconstructions with instrumental weather data.

64

65 **Study site**

66 Annaghbeg (53°22'58"N, 8°16'12"W) is a raised bog covering approximately 180 ha located
67 in eastern Co. Galway, Ireland, approximately 1.5 km west of the River Suck and 5 km to the
68 north of the town of Ballinasloe (see Figure 1). At Athenry, Co. Galway, 32 km west of the
69 site, mean annual temperature of 10 °C and mean annual rainfall of 1192 mm were recorded
70 for the period 1981-2010; at Gurteen, Co. Offaly, 38 km to the south east, mean annual
71 temperature of 9.8 °C and annual rainfall of 948 mm were recorded for the same period. The
72 site therefore lies close to the 1000 mm isohyet. Annaghbeg is designated a Natural Heritage

73 Area (NHA002344) and, despite some marginal peat cutting, retains a large area of intact
74 raised bog including a distinct dome with well-developed hummock-lawn-hollow
75 microtopography. Vegetation cover at the site includes *Calluna vulgaris*, *Eriophorum*
76 *vaginatum*, *Carex panicea* and *Rhynchospora* spp. and a range of *Sphagnum* mosses,
77 particularly on the dome. The existence of near-pristine microtopography and an intact dome
78 is now rare in Ireland, making Annaghbeg one of the few sites in Ireland suitable for this type
79 of study.

80

81 **Methods**

82 Three 50 cm deep cores were taken from a short transect across a single hummock–lawn–
83 hollow sequence on the intact dome of the study site (see Figure 2), one from each
84 microform. Cores were collected using a large diameter (15 cm \varnothing) Russian peat corer. Upon
85 completion of each borehole, the water table was allowed to equilibrate for 1 hour before the
86 depth below ground surface (bgs) of the contemporary water table was measured and
87 recorded.

88 In the laboratory, cores were described utilizing a simplified version of the Troels-Smith [47]
89 scheme. Each core was then divided in half lengthways and both halves were divided into
90 contiguous 1 cm thick slices of peat, yielding 47 slices from the hummock and 50 slices each
91 from the lawn and hollow. Samples from one half were used for ^{210}Pb dating, measured using
92 a Harwell Instruments BeGe gamma spectrometry, following the methods summarized in
93 Appleby [48], and Le Roux and Marshall [49]: each slice was weighed, air-dried at 50 °C
94 overnight, re-weighed, and homogenized using a pestle and mortar. Cumulative dry bulk
95 density (g cm^{-3}) was calculated to allow the Constant Rate of Supply (CRS) model [50] to be
96 applied. The homogenized samples were then packed into small plastic Petri dishes and

97 sealed with adhesive tape. Samples were then left for 21 days to allow ^{222}Rn - ^{214}Pb - ^{226}Ra
98 equilibration before being analyzed. In addition, the fall-out radionuclide ^{137}Cs was also
99 measured using the same detector to cross-validate resulting age models.

100 Samples from the other half of each core (every slice in the sections of the cores within the
101 limits of the ^{210}Pb age models and every other slice below those levels, resulting in analysis
102 of 39 slices from the hummock, 41 from the lawn and 50 from the hollow) were prepared for
103 testate amoebae analysis following standard methods outlined in Charman *et al.* [51].
104 Taxonomy followed that of Charman *et al.* [51] but with the modifications outlined by
105 Amesbury *et al.* [52] and the recent reclassification of *Nebela militaris* to the genus *Alabasta*
106 [53]. Reconstructed depth to water table (DWT) values were calculated using the European
107 testate amoebae transfer function [52], with sample-specific errors generated through 1000
108 bootstrap cycles [54]; to facilitate comparison between DWT records from the three
109 microforms, data were also converted to standardized residual z-scores. The resulting data
110 were explored numerically through the application of detrended correspondence analysis
111 (DCA) to explore underlying structure within the dataset [55] using the automatically
112 optimized number of ‘segments’ used for detrending generated by the PAST v3 software
113 package [56], and the Shannon-Wiener index was calculated for each sample as a measure of
114 alpha diversity using the same software.

115 To explore the influence of climatic variables on testate amoebae communities, the DWT
116 data were compared with instrumental weather data from Dublin (Phoenix Park) [57]; this
117 dataset comprises daily rainfall and maximum temperature measurements stretching from the
118 1880s to the present. The long time-series available from Dublin was preferred over the
119 geographically closer, but much shorter dataset from Gurteen, Co. Offaly, and the
120 discontinuous dataset from Athenry, Co. Galway – the former extending only back to the

121 1950s, and the latter missing data from substantial portions of the late-19th and mid-20th
122 centuries.

123

124 **Peat stratigraphy and chronology**

125 The simplified peat stratigraphy and surface topography of the three sampling locations is
126 represented graphically in Figure 2. Surface vegetation cover at the hummock sampling
127 location consisted of *Calluna vulgaris* with an understory comprised of *Sphagnum* sect.
128 *Acutifolia* and *Rhynchospora*; the uppermost 10 cm of acrotelmic peat consisted of the
129 unhumified remains of the same taxa (Tl¹3 Th⁰1 Tb+ Sh+, see Troels-Smith [47] for details
130 of classification symbols). Below this, to a depth of 24.5 cm bgs, was a layer of poorly
131 humified *Sphagnum* sect. *Acutifolia* peat with only traces of ericaceous stems and roots (Tb¹4
132 Tl+ Th+), which passed gradually into a moderate to well-humified herbaceous peat
133 (primarily remains of *Eriophorum*) with traces of *Sphagnum* and ericaceous stems/roots
134 (Th²33 Tl²1 Tb+ Sh+). At 41 cm bgs was a transition to moderately humified *Sphagnum*-
135 *Eriophorum* peat, again with traces of ericaceous remains, becoming more humified towards
136 the base of the core at 50 cm bgs (Tb³2, Th²2 Tl+ Sh+). The measured depth to water table
137 (DWT) was 18 cm.

138 The lawn sampling location was dominated by *Sphagnum* sect. *Acutifolia* mosses,
139 interspersed in the immediate vicinity (50 cm radius) with *Erica tetralix*, *Menyanthes*
140 *trifoliata*, and *Calluna vulgaris*. The upper portion of the core comprised moderate to well-
141 humified *Sphagnum* peat with a minor herbaceous component and rare ericaceous remains
142 (Tb³3 Tl²1 Sh+ Th+), with a gradual decrease in humification (to Tb¹3 Th²1 Tl+) towards the
143 base of the core at 50 cm bgs. DWT at the lawn sampling location was 10 cm.

144 At the hollow sampling location, surface vegetation consisted of *Sphagnum papillosum*
145 interspersed with *Menyanthes trifoliata* and *Drosera* spp. The uppermost 5.5 cm of the core
146 comprised unhumified *Sphagnum* moss with a minor component of *Menyanthes* (Tb⁰³ Th⁰¹);
147 beneath this, the remainder of the core, to a depth of 50 cm bgs, consisted of poorly-humified
148 *Sphagnum-Menyanthes* peat (Tb¹² Th¹² Sh+). The measured DWT at the hollow was 3 cm.

149 Age-depth models for all three cores, together with ¹³⁷Cs inventories are shown in Figure 3.
150 Full ²¹⁰Pb_{excess} inventories for the three cores are presented in the supplementary data
151 (Supplementary data 1). Utilizing the ²¹⁰Pb_{excess} data and the peat bulk density measurements,
152 the Constant Rate of Supply (CRS) age-depth model was applied to the hummock and lawn
153 cores. This model shows very similar accumulation rates for both profiles: 10-15 yrs cm⁻¹
154 during the late 19th century, increasing to ~2 yrs cm⁻¹ towards the top of both profiles. At
155 least part of the observed decrease in accumulation rate with depth may be attributed to
156 compression of the lower peats due to the weight of overlying strata [58]. Cross-validation of
157 these models utilizing the ¹³⁷Cs data, which would be expected to show two peaks – a larger
158 peak in the early 1960's relating to atmospheric nuclear weapons tests (peak in 1963), and a
159 smaller peak in the mid-1980's relating to the 1986 Chernobyl disaster [59] - suggests that
160 these models are robust. Cross-validation of the CRS age-depth model generated for the core
161 from the hollow microform was less satisfactory; the ¹³⁷Cs data from the hollow appear to be
162 offset, particularly the lower peak. The Constant Flux, Constant Sedimentation (CF-CS)
163 model [60], which does not utilize dry bulk density measurements and instead assumes a
164 steady rate of peat accumulation, performed better for the hollow core. Whilst many peat
165 sequences are unlikely to fulfill the prerequisite for the application of the CF-CS age-depth
166 model [49], a constant accumulation rate may be plausible for this short section of peat
167 formed in a hollow. Furthermore, practical difficulties in accurately measuring dry bulk
168 density in poorly humified saturated peat due to the potential for post-sampling evaporative

169 loss have previously been noted [5], and it is possible that errors in dry bulk density
170 measurements for the hollow core led to the poor performance of the CRS model. For this
171 reason, the CF-CS age-model is preferred for the hollow core; this model indicates a
172 generally constant peat accumulation rate of $\sim 4 \text{ yrs cm}^{-1}$ from the late 19th century onwards.

173

174 **Testate amoebae analysis**

175 Diagrams showing the relative abundance of testate amoebae (expressed as percentages in
176 each slice) from the three cores are shown in Figure 4 and are presented in the supplementary
177 data (Supplementary data 2), a minimum count of 100 tests was reached for each sample
178 (core level), with most samples from all microforms exceeding counts of 150 individual tests
179 [61]. A total of 31 taxa were observed in the cores of which 22 were encountered in at least
180 one sample from each of the three microforms. A list of taxa encountered in this study and
181 the abbreviations used in Figures 4 and 5 are given in Table 1.

182 **Table 1** List of testate amoebae taxa and abbreviations

Taxon name	Abbreviation	Microforms
<i>Alabasta militaris</i> type	NEB MIL	All
<i>Amphitrema wrightianum</i> type	AMP WRI	All
<i>Arcella arenaria</i> type	ARC ARE	All
<i>Arcella discoides</i> type	ARC DIS	All
<i>Archerella flavum</i>	ARC FLA	All
<i>Assulina muscorum</i> type	ASS MUS	All
<i>Assulina seminulum</i> type	ASS SEM	All
<i>Bulinularia indica</i>	BUL IND	All
<i>Centropyxis aculeata</i> type	CEN ACU	All
<i>Corythion-Trinema</i> type	COR TRI	All
<i>Cryptodifflugia sacculus</i> type	CRY SAC	All
<i>Cryptodifflugia oviformis</i> type	CRY OVI	Hummock and lawn only
<i>Cyclopyxis arcelloides</i> type	CYC ARC	All
<i>Difflugia acuminata</i> type	DIF ACU	Hummock only
<i>Difflugia leidyi</i>	DIF LEI	All
<i>Difflugia lucida</i> type	DIF LUC	All
<i>Difflugia oblonga</i> type	DIF OBL	All
<i>Euglypha ciliata</i> type	EUG CIL	All
<i>Euglypha rotunda</i> type	EUG ROT	All
<i>Heleopera petricola</i> type	HEL PET	All
<i>Heleopera rosea</i>	HEL ROS	All
<i>Heleopera sylvatica</i>	HEL SYL	All
<i>Hyalosphenia elegans</i>	HYA ELE	All
<i>Hyalosphenia papilio</i>	HYA PAP	Lawn and hollow only
<i>Hyalosphenia subflava</i>	HYA SUB	Hummock and hollow only
<i>Nebela carinata</i> type	NEB CAR	All
<i>Nebela collaris</i> type	NEB COL	Hollow only
<i>Nebela flabellulum</i>	NEB FLA	Hummock and lawn only
<i>Nebela tincta</i> type	NEB TIN	Hummock and lawn only
<i>Placocista spinosa</i>	PLA SPI	Hummock and lawn only
<i>Trigonopyxis arcula</i> type	TRI ARC	Hummock and lawn only

183

184 Assemblages from the hummock were dominated by *Cryptodifflugia sacculus* type and
 185 *Alabasta militaris* type, with smaller proportions of *Assulina* spp., *Cyclopyxis arcelloides*
 186 type, and *Heleopera sylvatica*. Other taxa that were important components of some
 187 assemblages from the hummock, but absent in other samples, were *Arcella arenaria* type,
 188 *Archerella flavum*, *Heleopera rosea* and *Trigonopyxis arcula* type, the latter two taxa
 189 increasing markedly in the upper 10 cm of the sequence.

190 Samples from the lawn show a shift from *Archerella flavum* and *Cryptodifflugia sacculus*
 191 type co-dominance below *c.*20 cm bgs, to the co-dominance of *Cryptodifflugia sacculus* type
 192 and *Cyclopyxis arcelloides* type towards the top of the sequence. Other taxa present in
 193 assemblages throughout the lawn sequence were *Difflugia lucida* type, *Alabasta militaris*
 194 type and *Hyalosphenia elegans*.

195 The hollow microform was characterized by assemblages dominated by *Archerella flavum*
 196 and *Amphitrema wrightianum* type along with smaller abundances of *Difflugia lucida* type
 197 and *Difflugia oblonga* type and occasional peaks in the abundance of *Heleopera petricola*
 198 type, *Assulina muscorum* type, and *Difflugia leidyi*.

199 **Table 2** Summary of reconstructed DWT values, generated using the Amesbury *et al.* [52]
 200 transfer function

	Measured water table depth (cm)	Mean DWT (cm)	σ	Max. DWT	Min. DWT	Range	Mean bootstrapped error estimate	σ
Hummock	18	18.8	4.2	27.7	12.3	15.4	7.8	0.021
Lawn	10	10.7	5.2	19.3	-2.1	21.4	7.7	0.018
Hollow	3	-1.9	1.7	1.3	-5.2	6.5	7.8	0.016

201

202 The taxa ordination plot from the DCA, shown in Figure 5a, is interpreted as showing a
 203 hydrological gradient with hygrophilous taxa such as *Difflugia leidyi* and *Hyalosphenia*
 204 *papilio* having high Axis 1 scores (eigenvalue = 0.58), and taxa generally regarded as
 205 xerophilous like *Trigonopyxis arcula* type plotting at the opposite end of the axis [6, 10, 17,
 206 18, 51]. This gradient is also reflected in the sample ordination, where Axis 1 sample scores
 207 have a strong negative correlation with reconstructed DWT values ($r = -0.98$, $p < 0.001$).
 208 Unsurprisingly, given the differences in testate amoebae assemblages and in the magnitude of
 209 DWT, samples from the different microforms cluster together in the sample ordination:
 210 samples from the hollow cluster tightly at the positive end of Axis 1, samples from the

211 hummock all have low Axis 1 scores, and show a wide range of Axis 2 scores (eigenvalue =
 212 0.18), whilst samples from the lawn plot in between the two, showing a wide spread along
 213 Axis 1.

214 **Table 3** Summary statistics for Shannon-Wiener diversity index (H')

	n	Mean	SD	Median	Variance
Hummock	39	2.217	0.305	2.252	0.052
Lawn	40	2.284	0.227	2.294	0.051
Hollow	50	1.829	0.222	1.853	0.049

215

216 The Shannon-Wiener diversity index (H') was calculated for all samples, and is shown, along
 217 with bootstrapped upper and lower estimates (999 cycles), in Figure 6. H' values for the
 218 dataset as a whole ranged between 1.17 and 2.69. Table 3 shows summary statistics for H'
 219 from the three different microforms. H' values have previously been used to indicate relative
 220 ecological stress, with values between 2.5 and 3.5 thought to indicate healthy environments,
 221 and values below 1.5 indicating stressed environments [62–65]; some samples from the
 222 hummock and lawn plot near to the lower limits of a 'healthy' environment, but many,
 223 including most samples from the hollow, appear to indicate some level of ecological stress.
 224 The Mann-Whitney pairwise test for equal population distributions showed that diversity was
 225 significantly lower for samples from the hollow than from the other two microforms, see
 226 Table 4.

227 **Table 4** Mann-Whitney pairwise test for equal population distributions. Lower half: Mann-
 228 Whitney U. Upper half: Bonferroni corrected *p* values. Hollow diversity is significantly
 229 different ($p < 0.01$) than hummock and lawn cores

	Hummock	Lawn	Hollow
Hummock		0.766	<0.001
Lawn	663.5		<0.001
Hollow	226	139.5	

230

231 **Water table reconstructions and instrumental weather data**

232 Figure 7a shows reconstructed DWT values from the three microforms plotted against
233 calendar year utilizing the best performing ^{210}Pb age-depth model (see above). Following the
234 recommendations of Amesbury *et al.* [52] to compensate for the differences in absolute
235 values between the three microforms and facilitate comparison between sequences, DWT
236 scores were converted to centered and standardized z-scores, shown in Figure 7b; this shows
237 good visual agreement between the three cores, especially from the mid-20th century
238 onwards. All three records show a marked drying trend from the 1950s until the mid-1960s,
239 followed by a shift towards wet conditions (decrease in DWT) in the early 1970s and a
240 prolonged drying trend throughout the 1980s and 1990s and into the 2000s.

241 In order to explore the relationships between testate amoebae-derived DWT values and
242 climatic forcing, DWT z-scores were compared with instrumental weather data from Dublin
243 (Phoenix Park). To this end, the approach of Charman *et al.* [46] was adopted: all data were
244 converted to decadal averages and correlation coefficients between z-scores and weather data
245 were calculated. In order to analyze the effects of long-term climatic variability, correlations
246 with climate data averaged over the contemporary decade plus the preceding 10 and 20 years
247 were also calculated. Correlations are shown in Table 5, variables showing significant
248 correlations are plotted on Figure 7c-e.

249 **Table 5** Correlations between DWT z-scores and instrumental weather data from Dublin.
 250 Instrumental weather data were decadal averages from 1880s to 2010s; data were also
 251 averaged over the contemporary decade and the preceding 10 (+10) and 20 (+20) years. JJA
 252 = June, July, August; DJF = December, January, February. Statistically significant
 253 correlations are highlighted in bold, * = $p < 0.05$, ** = $p < 0.01$. Only variables with at least one
 254 significant correlation are shown

	Hummock	Lawn	Hollow
Annual Temp	0.63*	0.67*	0.18
Annual Temp +10	0.63*	0.69*	0.32
Annual Temp +20	0.54	0.70*	0.35
JJA Temp	0.39	0.46	-0.00
JJA Temp +10	0.47	0.57	0.27
JJA Temp +20	0.43	0.62*	0.30
DJF Temp	0.76**	0.62*	0.11
DJF Temp +10	0.68*	0.60*	0.27
DJF Temp +20	0.50	0.53	0.39
JJA Precip	-0.47	-0.14	0.02
JJA Precip +10	-0.54	-0.25	0.11
JJA Precip +20	-0.85**	-0.69*	-0.29

255

256 In common with the findings of similar studies, testate amoebae-derived DWT data showed
 257 statistically significant positive correlations with temperature variables and significant
 258 negative correlations with summer precipitation [41, 45, 46]. Although, as expected,
 259 significant relationships were observed between the DWT and summer precipitation data,
 260 significant correlations were not obtained with annual precipitation data. This discrepancy
 261 can probably be accounted for by the distance between location of the weather station on the
 262 east coast of Ireland and the study site. Precipitation variables are generally less spatially
 263 ‘smooth’ than temperature, and, as noted above, the study site is located near to the 1000mm
 264 isohyet which runs approximately parallel with the Atlantic (west) coast of Ireland; therefore
 265 precipitation patterns at Dublin may provide a poor analogue for those at Annaghbeg. The
 266 patchy temporal coverage of data (i.e. few datapoints at the decadal scale) from stations
 267 closer to the site prevented the identification of statistically significant relationships. No
 268 statistically-significant correlations were obtained between the weather data and DWT from

269 the hollow, in contrast with the records from the hummock and hollow which both showed
270 similar patterns in terms of climatic forcing.

271

272 **Discussion**

273 As expected, this study has shown that there are significant differences in testate amoeba
274 community composition and structure between different bog microforms. These differences
275 manifested in the presence/absence of certain key taxa – e.g. the presence of *Hyalosphenia*
276 *papilio* in the hollow and its absence in the hummock, and the opposite pattern for
277 *Trigonopyxis arcula* type – as well as in differences in dominant taxa - *Cryptodiffugia*
278 *sacculus* type and *Alabasta militaris* type in the hummock, *Archerella flavum* and
279 *Amphitrema wrightianum* type in the hollow. This confirms the findings of numerous
280 previous studies [e.g. 2, 3, 6, 10, 17, 18], and serves to underline the value of testate amoebae
281 as environmental indicators.

282 There were also important differences between microforms in the structure of their respective
283 testate amoeba communities. Alpha diversity was found to be significantly lower in the
284 hollow microform than in either the lawn or hummock. A similar pattern was observed by
285 Marcisz *et al.* [33, 66], although other studies have noted the opposite [31, 32]. The lower
286 species richness in the hollow may indicate that stresses other than water availability, for
287 example prey scarcity, have a greater effect on testate amoebae communities in hollows than
288 in other microforms [13, 18, 19, 31].

289 Several studies in the past have suggested that the co-occurrence of certain testate amoebae
290 taxa, especially those seemingly at opposite ends of the hydrological gradient, might be
291 indicative of highly variable moisture conditions in some sampling locations [4, 5, 13, 35,
292 67]. This pattern was confirmed by the findings of Sullivan and Booth [34], who found that

293 increased abundance of certain taxa, especially *Arcella discoides*, *Diffflugia pulex* and
294 *Hyalosphenia subflava*, were associated with higher short-term environmental variability. It
295 is notable that in the hollow microform, the combined abundances of these taxa rarely
296 exceeded 1-2% of the entire assemblage (max. 7.6%, median 0.7%), but were much higher in
297 the lawn (max. 45.7%, median 20.8%) and hummock (max. 54.3%, median 22.5%). Note that
298 *D. pulex* is here included within *Cryptodiffflugia sacculus* type [52], although most
299 individuals encountered in this study would refer to *D. pulex*. This finding therefore supports
300 the conclusions of previous studies which have suggested that testate amoebae communities
301 in hummocks and lawns might be more sensitive to changes in hydrological conditions than
302 those inhabiting hollows [33, 44], at least insofar as this sensitivity is measurable based on
303 the relative proportions taxa that can be reliably distinguished in paleoecological
304 assemblages.

305 As would be expected given the differences in testate amoebae community composition and
306 structure, testate amoebae-derived DWT reconstructions, based on the most recent European
307 transfer function [52], also differed in absolute magnitude – hummock DWT had the highest
308 mean values (i.e. driest) and mean hollow DWT the lowest (wettest), with mean lawn DWT
309 being intermediate between the two. DWT values from the lawn showed the greatest
310 variability in terms of range of absolute values, closely followed by the hummock, with the
311 hummock displaying the smallest range in DWT. It has previously been pointed out that
312 despite the greater sensitivity of hummock and lawn testate amoebae communities to
313 environmental change, species tolerances and prediction errors in transfer function models
314 were typically larger for such assemblages [33]. Application of the new pan-European
315 transfer function [52], based on a vastly expanded training set relative to previous models,
316 appears to have addressed this issue, with no significant differences in bootstrapped
317 prediction errors between microforms. Although conversion of the absolute DWT values to z-

318 scores largely removed these differences between microforms, comparisons between DWT z-
319 scores and instrumental weather data still appeared to show that the hollow is less responsive
320 to environmental forcing than the other two microforms.

321 Visual assessment of the three DWT curves appears to indicate similar patterns of change
322 recorded by testate amoebae in all three microforms - especially a marked wet shift in the
323 early 1970s followed by prolonged drying from the 1980s onwards, thus broadly supporting
324 the notion that bog surface wetness in all parts of a peat bog will tend to respond in the same
325 direction to climatic forcing [38, 39] – however, the hollow did not show any statistically
326 significant relationships with climate data. In contrast, both the hummock and lawn showed
327 statistically significant correlations with annual and winter temperature and summer
328 precipitation, with the lawn additionally being significantly correlated with summer
329 temperature. The relationships between these water table reconstructions agree with the
330 findings of previous studies, supporting the notion that testate amoebae communities are
331 sensitive indicators of past climatic conditions [41, 45, 46].

332 The high diversity in testate communities from the lawn microform and the strong
333 correlations obtained between lawn DWT and climate variables may lend some support to the
334 recommendation that intermediate microforms should be sampled to contain the most
335 climatically-sensitive record of past hydrological change [68–70]. However, the similarly
336 high testate amoebae diversity in the hummock microform and significant correlations with
337 instrumental temperature and precipitation variables presents a challenge to the assumption
338 that hummocks record a ‘complacent’ climatic signal [43, 69], at least in terms of testate
339 amoebae, if not other proxy indicators such as peat humification or plant macrofossils [71–
340 74].

341 Careful selection of sampling location with respect to bog microtopography clearly does have
342 an impact on the climatic signal recorded by fossil testate amoebae. This study shows that
343 whilst testate amoebae communities in all microforms seem to respond in the same direction
344 to climatic forcing, this response was found to be muted in the hollow community compared
345 with the lawn and hummock. The differences in climatic sensitivity illustrated here should be
346 taken into account in future paleoecological studies. Testate amoebae sequences taken
347 through hollow microforms may appear to record less climatically-driven hydrological
348 variability than is really the case.

349

350 **Conclusions**

351 Testate amoebae community composition at Annaghbeg bog, Co. Galway, Ireland, was
352 strongly affected by bog microtopography; the hummock, lawn and hollow microforms
353 contained distinct assemblages, and those in the hollow were significantly less diverse than in
354 the other microforms. Reconstructed DWT values from each of the microforms differed in
355 absolute terms, although bootstrapped prediction errors were similar for all three sequences.
356 Visual comparison of standardized DWT data plotted against independent age-depth models
357 showed similar trends over the last ~130 yrs, supporting the notion that bog surface wetness
358 in all microforms respond in the same general direction to climate forcing [38, 39]. When
359 compared to a long instrumental weather timeseries from Dublin, reconstructed DWT from
360 both the hummock and lawn showed statistically significant correlations with temperature
361 (annual and winter) and summer precipitation variables, but no statistically significant
362 relationships were observed between hollow DWT and any climate variables. Given the
363 lower diversity, smaller variability in DWT, and weaker relationships with climatic variables,
364 it appears that hollows may therefore be less suited to paleoecological reconstruction than

365 other microforms. This is because water availability (the principal variable of interest in
366 peatland paleoecological studies [3, 5, 16, 28, 52, 75–77]) may be a relatively minor stress on
367 testate amoebae communities in hollows compared with other factors such as prey scarcity
368 [13, 18, 19, 31]; in contrast, testate amoebae communities in hummocks and hollows appear
369 to be more strongly controlled by water availability. Whilst the suggestion that sampling for
370 paleoecological investigations should target intermediate bog microforms appears to be sound
371 [68], the assertion that hummocks are ‘climatically-complacent’ [43], at least in terms of the
372 testate amoebae communities they support, is challenged.

373

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Fig. 1 a: map of Ireland showing site location; b: sampling location; c: general view of the dome of Annaghbeg

Fig. 2. Composite cross section showing simplified peat stratigraphy and surface topography.

Peat composition based on Troels-Smith [47] (Tb = moss peat, Th = herbaceous peat, Tl = ericaceous or woody peat) and humification estimated qualitatively on a scale of 0-4 (0 = fresh vegetation, 4 = totally humified)

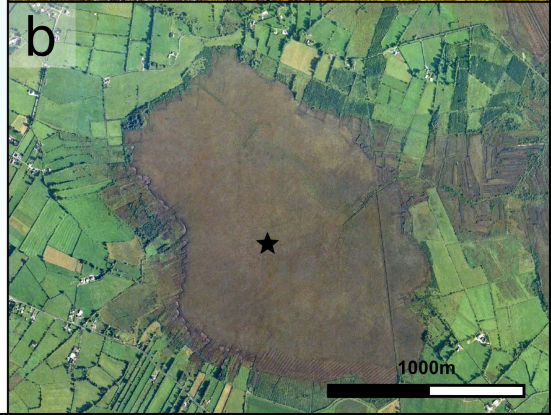
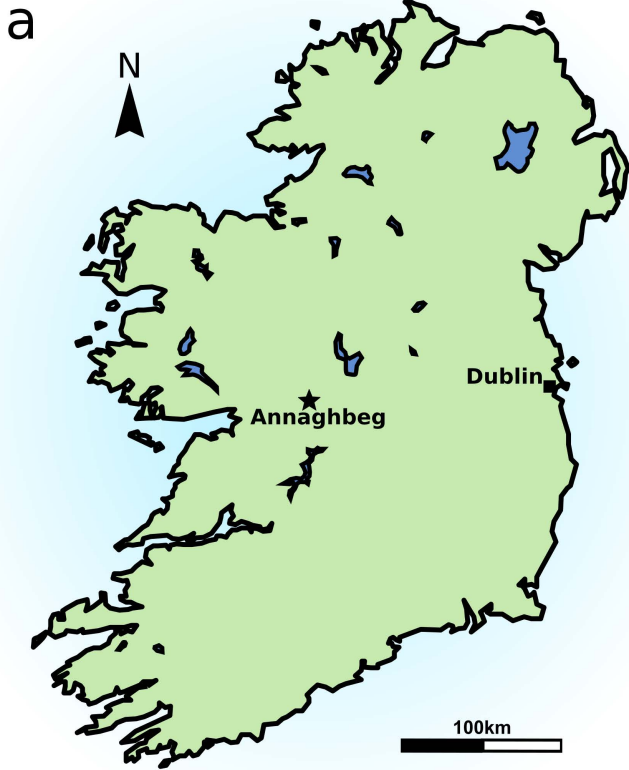
Fig. 3 a: age-depth models for the three short cores from Annaghbeg. Solid line = hummock; dotted line = lawn; dashed line = hollow. b: ^{137}Cs inventories plotted against depth in cm

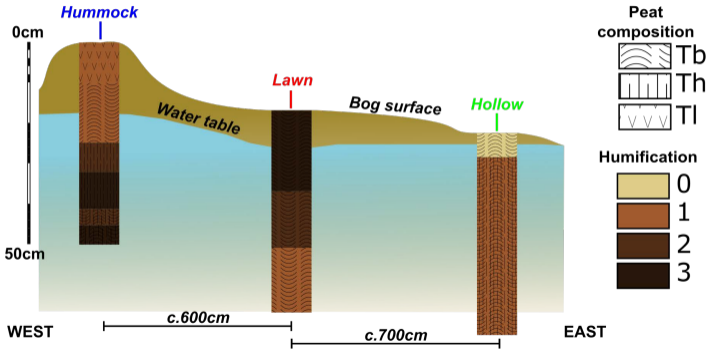
Fig. 4 Diagrams showing relative abundance of testate amoebae, expressed as percentages, from the three short cores from Annaghbeg; a: hummock; b: lawn; c: hollow. Reconstructed DWT values were generated using the Amesbury *et al.* [52] transfer function, with sample specific errors generated using 1000 bootstrap cycles (error bars). See Table 1 for taxon abbreviations

Fig. 5 Detrended correspondence analysis (DCA), 26 segments. a: taxa ordination, see Table 1 for abbreviations. b: sample ordination, each sample representing a 1 cm thick slice of core

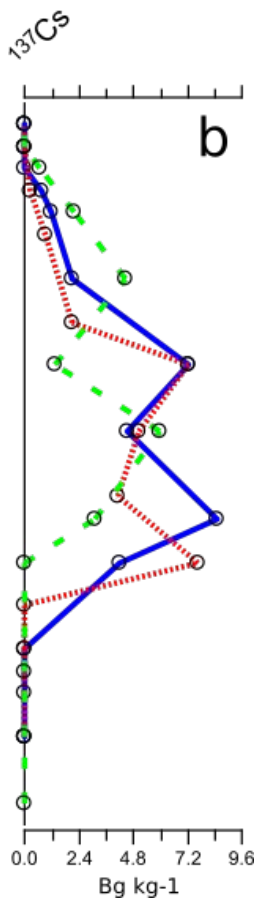
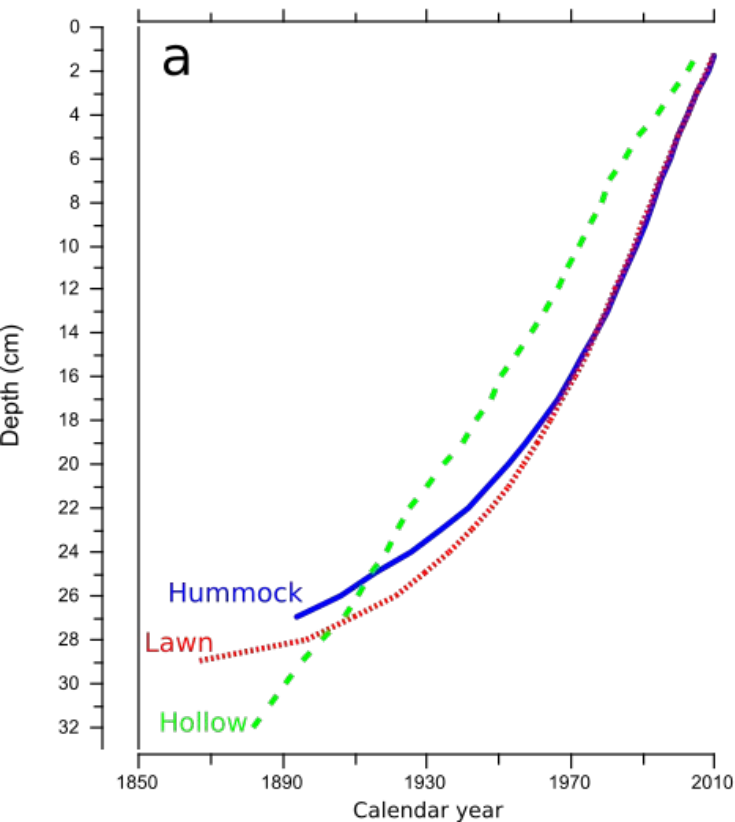
Fig. 6 Shannon-Wiener diversity indices (H') plotted against calendar year. Error bars indicate bootstrapped upper and lower estimates (999 bootstrap cycles)

Fig. 7 a: reconstructed DWT plotted against age-depth models (thick lines), shaded bands indicate bootstrapped errors. b: DWT data converted to z-scores (centered and standardized); c-e: instrumental weather data from Dublin (Phoenix Park), showing decadal averages (pale grey), data averaged over contemporary decade and preceding 10 years (mid tone) and 20 years (black).

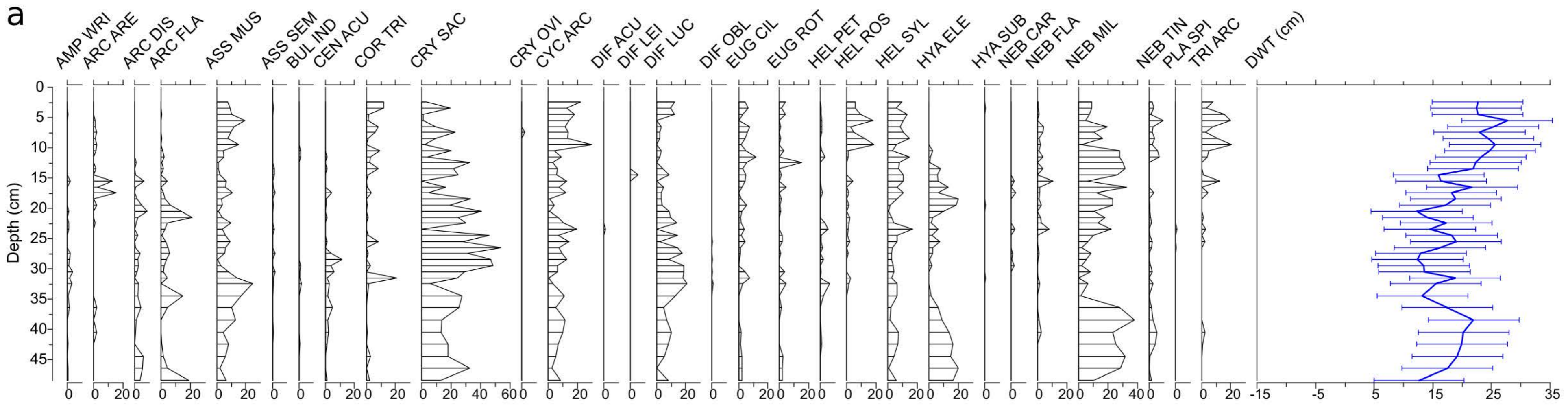




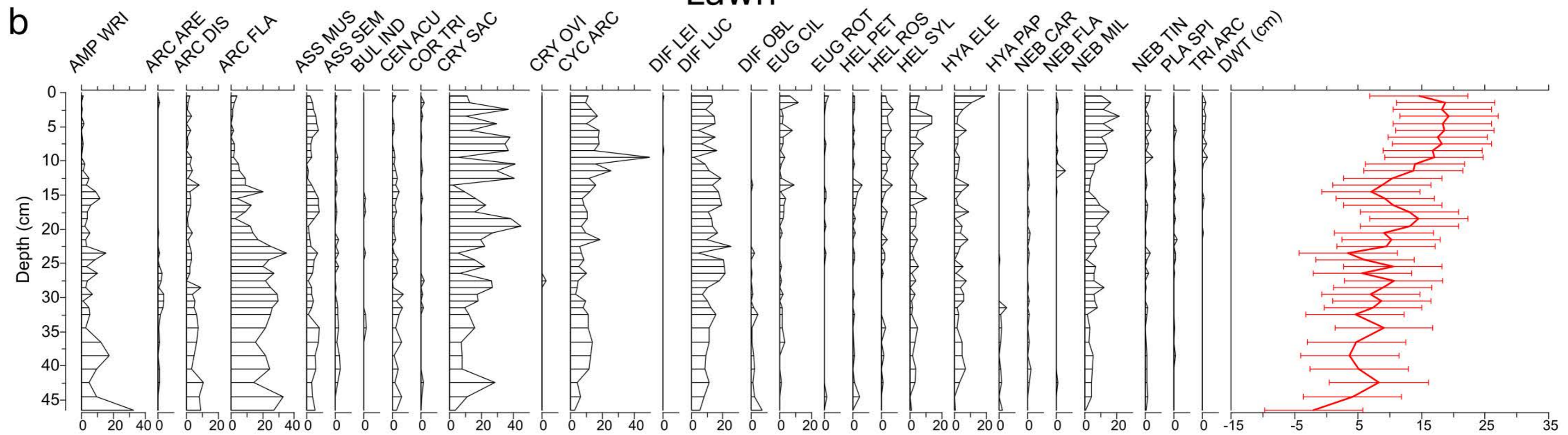
Age-depth models



Hummock



Lawn



Hollow

