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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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Abstract

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

Key words

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

Introduction

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

The issue of how differences in peatland surface microtopography affect species-environment relationships is another under-researched area. Since the falsification [38, 39] of the ‘cyclic’ model of bog growth [40], that posited a largely autogenic natural alternation between hummock and hollow surface microforms as the main driver of peat formation, it has been generally accepted that bog surface wetness is substantially affected by climatic forcing [41]. Nevertheless, there remains a suspicion that not all surface microforms are equally responsive to climatic variability, and that hummocks, which have often been shown to be persistent features [39, 42], may be “climatically-complacent” [43]. Although surface microforms have long been known to host distinct testate amoebae communities [6, 18], to date only a few studies have directly investigated variability in response of testate amoebae-environment responses in relation to bog microtopography [34, 44].

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

Study site

Annaghbeg (53º22'58"N, 8º16'12"W) is a raised bog covering approximately 180 ha located in eastern Co. Galway, Ireland, approximately 1.5 km west of the River Suck and 5 km to the north of the town of Ballinasloe (see Figure 1). At Athenry, Co. Galway, 32 km west of the site, mean annual temperature of 10 °C and mean annual rainfall of 1192 mm were recorded for the period 1981-2010; at Gurteen, Co. Offaly, 38 km to the south east, mean annual temperature of 9.8 °C and annual rainfall of 948 mm were recorded for the same period. The site therefore lies close to the 1000 mm isohyet. Annaghbeg is designated a Natural Heritage

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

Methods

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

In the laboratory, cores were described utilizing a simplified version of the Troels-Smith [47] scheme. Each core was then divided in half lengthways and both halves were divided into contiguous 1 cm thick slices of peat, yielding 47 slices from the hummock and 50 slices each from the lawn and hollow. Samples from one half were used for ^{210}Pb dating, measured using a Harwell Instruments BeGe gamma spectrometry, following the methods summarized in Appleby [48], and Le Roux and Marshall [49]: each slice was weighed, air-dried at 50 ºC overnight, re-weighed, and homogenized using a pestle and mortar. Cumulative dry bulk density (g cm $^{-3}$) was calculated to allow the Constant Rate of Supply (CRS) model [50] to be applied. The homogenized samples were then packed into small plastic Petri dishes and sealed with adhesive tape. Samples were then left for 21 days to allow ^{222}Rn-^{214}Pb-^{226}Ra equilibration before being analyzed. In addition, the fall-out radionuclide ^{137}Cs was also measured using the same detector to cross-validate resulting age models.

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

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

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

Peat stratigraphy and chronology

The simplified peat stratigraphy and surface topography of the three sampling locations is represented graphically in Figure 2. Surface vegetation cover at the hummock sampling location consisted of *Calluna vulgaris* with an understory comprised of *Sphagnum* sect. *Acutifolia* and *Rhynchospora*; the uppermost 10 cm of acrotelmic peat consisted of the unhumified remains of the same taxa ($Tl^1 3$ $Th^0 1$ Tb+ Sh+, see Troels-Smith [47] for details of classification symbols). Below this, to a depth of 24.5 cm bgs, was a layer of poorly humified *Sphagnum* sect. *Acutifolia* peat with only traces of ericaceous stems and roots ($Tb^1 4$ Tl+ Th+), which passed gradually into a moderate to well-humified herbaceous peat (primarily remains of *Eriophorum*) with traces of *Sphagnum* and ericaceous stems/roots ($Th^{2/3} 3$ $Tl^2 1$ Tb+ Sh+). At 41 cm bgs was a transition to moderately humified *Sphagnum*-*Eriophorum* peat, again with traces of ericaceous remains, becoming more humified towards the base of the core at 50 cm bgs ($Tb^3 2$, $Th^2 2$ Tl+ Sh+). The measured depth to water table (DWT) was 18 cm.

The lawn sampling location was dominated by *Sphagnum* sect. *Acutifolia* mosses, interspersed in the immediate vicinity (50 cm radius) with *Erica tetralix*, *Menyanthes trifoliata*, and *Calluna vulgaris*. The upper portion of the core comprised moderate to well-humified *Sphagnum* peat with a minor herbaceous component and rare ericaceous remains ($Tb^3 3$ $Tl^2 1$ Sh+ Th+), with a gradual decrease in humifaction (to $Tb^1 3$ $Th^2 1$ Tl+) towards the base of the core at 50 cm bgs. DWT at the lawn sampling location was 10 cm.

At the hollow sampling location, surface vegetation consisted of *Sphagnum papillosum* interspersed with *Menyanthes trifoliata* and *Drosera* spp. The uppermost 5.5 cm of the core comprised unhumified *Sphagnum* moss with a minor component of *Menyanthes* ($Tb^0 3$ $Th^0 1$); beneath this, the remainder of the core, to a depth of 50 cm bgs, consisted of poorly-humified *Sphagnum-Menyanthes* peat ($Tb^1 2$ $Th^1 2$ Sh+). The measured DWT at the hollow was 3 cm.

Age-depth models for all three cores, together with ^{137}Cs inventories are shown in Figure 3. Full ^{210}Pb$_{excess}$ inventories for the three cores are presented in the supplementary data (Supplementary data 1). Utilizing the ^{210}Pb$_{excess}$ data and the peat bulk density measurements, the Constant Rate of Supply (CRS) age-depth model was applied to the hummock and lawn cores. This model shows very similar accumulation rates for both profiles: 10-15 yrs cm^{-1} during the late 19th century, increasing to ~2 yrs cm^{-1} towards the top of both profiles. At least part of the observed decrease in accumulation rate with depth may be attributed to compression of the lower peats due to the weight of overlying strata [58]. Cross-validation of these models utilizing the ^{137}Cs data, which would be expected to show two peaks – a larger peak in the early 1960's relating to atmospheric nuclear weapons tests (peak in 1963), and a smaller peak in the mid-1980's relating to the 1986 Chernobyl disaster [59] - suggests that these models are robust. Cross-validation of the CRS age-depth model generated for the core from the hollow microform was less satisfactory; the ^{137}Cs data from the hollow appear to be offset, particularly the lower peak. The Constant Flux, Constant Sedimentation (CF-CS) model [60], which does not utilize dry bulk density measurements and instead assumes a steady rate of peat accumulation, performed better for the hollow core. Whilst many peat sequences are unlikely to fulfill the prerequisite for the application of the CF-CS age-depth model [49], a constant accumulation rate may be plausible for this short section of peat formed in a hollow. Furthermore, practical difficulties in accurately measuring dry bulk density in poorly humified saturated peat due to the potential for post-sampling evaporative loss have previously been noted [5], and it is possible that errors in dry bulk density measurements for the hollow core led to the poor performance of the CRS model. For this reason, the CF-CS age-model is preferred for the hollow core; this model indicates a generally constant peat accumulation rate of ~4 yrs cm^{-1} from the late 19th century onwards.

Testate amoebae analysis

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

Table 1 List of testate amoebae taxa and abbreviations

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

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

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

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

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

The taxa ordination plot from the DCA, shown in Figure 5a, is interpreted as showing a hydrological gradient with hygrophilous taxa such as *Difflugia leidyi* and *Hyalosphenia papilio* having high Axis 1 scores (eigenvalue = 0.58), and taxa generally regarded as xerophilous like *Trigonopyxis arcula* type plotting at the opposite end of the axis [6, 10, 17, 18, 51]. This gradient is also reflected in the sample ordination, where Axis 1 sample scores have a strong negative correlation with reconstructed DWT values (r = -0.98, p<0.001). Unsurprisingly, given the differences in testate amoebae assemblages and in the magnitude of DWT, samples from the different microforms cluster together in the sample ordination: samples from the hollow cluster tightly at the positive end of Axis 1, samples from the hummock all have low Axis 1 scores, and show a wide range of Axis 2 scores (eigenvalue = 0.18), whilst samples from the lawn plot in between the two, showing a wide spread along Axis 1.

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

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

Table 4 Mann-Whitney pairwise test for equal population distributions. Lower half: Mann-Whitney U. Upper half: Bonferroni corrected *p* values. Hollow diversity is significantly 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	

Water table reconstructions and instrumental weather data

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

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

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

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

Discussion

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

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

Several studies in the past have suggested that the co-occurrence of certain testate amoebae taxa, especially those seemingly at opposite ends of the hydrological gradient, might be indicative of highly variable moisture conditions in some sampling locations [4, 5, 13, 35, 67]. This pattern was confirmed by the findings of Sullivan and Booth [34], who found that increased abundance of certain taxa, especially *Arcella discoides*, *Difflugia pulex* and *Hyalosphenia subflava*, were associated with higher short-term environmental variability. It is notable that in the hollow microform, the combined abundances of these taxa rarely exceeded 1-2% of the entire assemblage (max. 7.6%, median 0.7%), but were much higher in the lawn (max. 45.7%, median 20.8%) and hummock (max. 54.3%, median 22.5%). Note that *D. pulex* is here included within *Cryptodifflugia sacculus* type [52], although most individuals encountered in this study would refer to *D. pulex*. This finding therefore supports the conclusions of previous studies which have suggested that testate amoebae communities in hummocks and lawns might be more sensitive to changes in hydrological conditions than those inhabiting hollows [33, 44], at least insofar as this sensitivity is measurable based on the relative proportions taxa that can be reliably distinguished in paleoecological assemblages.

As would be expected given the differences in testate amoebae community composition and structure, testate amoebae-derived DWT reconstructions, based on the most recent European transfer function [52], also differed in absolute magnitude – hummock DWT had the highest mean values (i.e. driest) and mean hollow DWT the lowest (wettest), with mean lawn DWT being intermediate between the two. DWT values from the lawn showed the greatest variability in terms of range of absolute values, closely followed by the hummock, with the hummock displaying the smallest range in DWT. It has previously been pointed out that despite the greater sensitivity of hummock and lawn testate amoebae communities to environmental change, species tolerances and prediction errors in transfer function models were typically larger for such assemblages [33]. Application of the new pan-European transfer function [52], based on a vastly expanded training set relative to previous models, appears to have addressed this issue, with no significant differences in bootstrapped prediction errors between microforms. Although conversion of the absolute DWT values to z-scores largely removed these differences between microforms, comparisons between DWT z-scores and instrumental weather data still appeared to show that the hollow is less responsive to environmental forcing than the other two microforms.

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

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

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

Conclusions

Testate amoebae community composition at Annaghbeg bog, Co. Galway, Ireland, was strongly affected by bog microtopography; the hummock, lawn and hollow microforms contained distinct assemblages, and those in the hollow were significantly less diverse than in the other microforms. Reconstructed DWT values from each of the microforms differed in absolute terms, although bootstrapped prediction errors were similar for all three sequences. Visual comparison of standardized DWT data plotted against independent age-depth models showed similar trends over the last ~130 yrs, supporting the notion that bog surface wetness in all microforms respond in the same general direction to climate forcing [38, 39]. When compared to a long instrumental weather timeseries from Dublin, reconstructed DWT from both the hummock and lawn showed statistically significant correlations with temperature (annual and winter) and summer precipitation variables, but no statistically significant relationships were observed between hollow DWT and any climate variables. Given the lower diversity, smaller variability in DWT, and weaker relationships with climatic variables, it appears that hollows may therefore be less suited to paleoecological reconstruction than other microforms. This is because water availability (the principal variable of interest in peatland paleoecological studies [3, 5, 16, 28, 52, 75–77]) may be a relatively minor stress on testate amoebae communities in hollows compared with other factors such as prey scarcity [13, 18, 19, 31]; in contrast, testate amoebae communities in hummocks and hollows appear to be more strongly controlled by water availability. Whilst the suggestion that sampling for paleoecological investigations should target intermediate bog microforms appears to be sound [68], the assertion that hummocks are ‘climatically-complacent’ [43], at least in terms of the testate amoebae communities they support, is challenged.

References

1. Beyens L, Chardez D (1984) Testate Amoebae (Rhizopoda, Testaceae) from South-West Ireland. Arch Für Protistenkd 128:109–126. https://doi.org/10.1016/S0003-9365(84)80033-0

2. Bobrov AA, Charman DJ, Warner BG (1999) Ecology of testate amoebae (Protozoa: Rhizopoda) on peatlands in western Russia with special attention to niche separation in closely related taxa. Protist 150:125–136

3. Booth RK (2002) Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: modern ecology and hydrological calibration. J Paleolimnol 28:329–348

4. Booth RK, Sullivan ME, Sousa VA (2008) Ecology of testate amoebae in a North Carolina pocosin and their potential use as environmental and paleoenvironmental indicators. Ecoscience 15:277–289. https://doi.org/10.2980/15-2-3111

5. Charman DJ, Blundell A, ACCROTELM Members (2007) A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands. J Quat Sci 22:209–221. https://doi.org/10.1002/jqs.1026

6. De Graaf F (1956) Studies on Rotaria and Rhizopoda from the Netherlands. Bioloisch Jaarb Dodonea 23:145–217

7. Escobar J, Martínez JI, Parra LN (2005) THECAMOEBIANS (TESTACEOUS RHIZOPODS) FROM A TROPICAL LAKE: LA FE RESERVOIR, ANTIOQUIA, COLOMBIA. Caldasia 27:293–298

8. Grospietsch Th (1953) Rhizopodenanalytische Untersuchungen an Mooren Ostholsteins. Arch Für Hydrobiol 47:321–452

9. Heal OW (1962) The abundance and microdistribution of testate amoebae (Protozoa: Rhizopoda) in Sphagnum. Oikos 13:35–47

10. Heal OW (1961) The distribution of testate amoebae (Rhizopoda: Testacea) in some fens and bogs in northern England. J Linn Soc Zool 44:369–382

11. Jassey VEJ, Chiapusio G, Mitchell EAD, et al (2011) Fine-Scale Horizontal and Vertical Micro-distribution Patterns of Testate Amoebae Along a Narrow Fen/Bog Gradient. Microb Ecol 61:374–385. https://doi.org/10.1007/s00248-010-9756-9

12. Lamentowicz M, Lamentowicz Ł, Knaap WO, et al (2009) Contrasting Species—Environment Relationships in Communities of Testate Amoebae, Bryophytes and Vascular Plants Along the Fen–Bog Gradient. Microb Ecol 59:499–510. https://doi.org/10.1007/s00248-009-9617-6

13. Lamentowicz M, Mitchell EAD (2005) The Ecology of Testate Amoebae (Protists) in Sphagnum in North-western Poland in Relation to Peatland Ecology. Microb Ecol 50:48–63. https://doi.org/10.1007/s00248-004-0105-8

14. Mazei YuA, Tsyganov AN, Bubnova OA (2007) Structure of a community of testate amoebae in a sphagnum dominated bog in upper sura flow (Middle Volga Territory). Biol Bull 34:382–394. https://doi.org/10.1134/S1062359007040115

15. Meisterfeld R (1977) Die horizontale und vertikale Verteilung der Testaceen (Rhizopden, Testecea) in Sphagnum. Arch Für Hydrobiol 79:319–356

16. Swindles GT, Charman DJ, Roe HM, Sansum PA (2009) Environmental controls on peatland testate amoebae (Protozoa: Rhizopoda) in the North of Ireland: Implications for Holocene palaeoclimate studies. J Paleolimnol 42:123–140. https://doi.org/10.1007/s10933-008-9266-7

17. Tolonen K (1986) Rhizopod analysis. In: Berglund BE (ed) Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, Chichester

18. Tolonen K, Warner BG, Vasander H (1992) Ecology of testaceans (Protozoa: Rhizopoda) in mires in southern Finland: 1. Autecology. Arch Für Protistenkd 142:119–138

19. Tsyganov AN, Aerts R, Nijs I, et al (2012) Sphagnum-dwelling Testate Amoebae in Subarctic Bogs are More Sensitive to Soil Warming in the Growing Season than in Winter: the Results of Eight-year Field Climate Manipulations. Protist 163:400–414. https://doi.org/10.1016/j.protis.2011.07.005

20. Charman DJ (1997) Modelling hydrological relationships of testate amoebae (Protozoa: Rhizopoda) on New Zealand peatlands. J R Soc N Z 27:465. https://doi.org/10.1080/03014223.1997.9517549

21. Charman DJ, Warner BG (1992) Relationship between testate amoebae (Protozoa: Rhizopoda) and microenvironmental parameters on a forested peatland in northeastern Ontario. Can J Zool 70:2474–2482. https://doi.org/10.1139/z92-331

22. Woodland WA, Charman DJ, Sims PC (1998) Quantitative estimates of water tables and soil moisture in Holocene peatlands from testate amoebae. The Holocene 8:261–273. https://doi.org/10.1191/095968398667004497

23. Amesbury MJ, Charman DJ, Fyfe RM, et al (2008) Bronze Age upland settlement decline in southwest England: testing the climate change hypothesis. J Archaeol Sci 35:87–98

24. Charman DJ (2010) Centennial climate variability in the British Isles during the mid-late Holocene. Quat Sci Rev 29:1539–1554

25. Gearey B, Caseldine C (2006) Archaeological applications of testate amoebae analyses: a case study from Derryville, Co. Tipperary, Ireland. J Archaeol Sci 33:49–55

26. Mitchell EAD, Charman DJ, Warner BG (2008) Testate amoebae analysis in ecological and paleoecological studies of wetlands: past, present and future. Biodivers Conserv 17:2115–2137. https://doi.org/10.1007/s10531-007-9221-3

27. Plunkett G, Whitehouse NJ, Hall VA, et al (2009) A multi-proxy palaeoenvironmental investigation of the findspot of an Iron Age bog body from Oldcroghan, Co. Offaly, Ireland. J Archaeol Sci 36:265–277

28. Swindles GT, Lawson IT, Matthews I, et al (2013) Centennial-scale climate change in Ireland during the Holocene. Earth Sci Rev 126:300–320

29. Swindles GT, Blundell A, Roe HM, Hall VA (2010) A 4500-year proxy climate record from peatlands in the North of Ireland: the identification of widespread summer 'drought phases'? Quat Sci Rev 29:1577–1589

30. Stastney P, Young DS, Branch NP (2018) The identification of late-Holocene bog bursts at Littleton Bog, Ireland: Ecohydrological changes display complex climatic and non-climatic drivers: The Holocene 28:570–582. https://doi.org/10.1177/0959683617735581

31. Mieczan T (2010) Vertical Micro-Zonation of Testate Amoebae and Ciliates in Peatland Waters in Relation to Potential Food Resources and Grazing Pressure. Int Rev Hydrobiol 95:86–102. https://doi.org/10.1002/iroh.200911188

32. Roe HM, Elliott SM, Patterson RT (2017) Re-assessing the vertical distribution of testate amoeba communities in surface peats: Implications for palaeohydrological studies. Eur J Protistol 60:13–27. https://doi.org/10.1016/j.ejop.2017.03.006

33. Marcisz K, Fournier B, Gilbert D, et al (2014) Response of Sphagnum Peatland Testate Amoebae to a 1-Year Transplantation Experiment Along an Artificial Hydrological Gradient. Microb Ecol 67:810–818. https://doi.org/10.1007/s00248-014-0367-8

34. Sullivan ME, Booth RK (2011) The Potential Influence of Short-term Environmental Variability on the Composition of Testate Amoeba Communities in Sphagnum Peatlands. Microb Ecol 62:80–93. https://doi.org/10.1007/s00248-011-9875-y

35. Talbot J, Richard PJH, Roulet NT, Booth RK (2010) Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence. J Veg Sci 21:143–156. https://doi.org/10.1111/j.1654-1103.2009.01128.x

36. Barber K, Maddy D, Rose N, et al (2000) Replicated proxy-climate signals over the last 2000 yr from two distant UK peat bogs: new evidence for regional palaeoclimate teleconnections. Quat Sci Rev 19:481–487

37. Charman DJ, Blundell A, Chiverrell RC, et al (2006) Compilation of non-annually resolved Holocene proxy climate records: stacked Holocene peatland palaeo-water table reconstructions from northern Britain. Quat Sci Rev 25:336–350. https://doi.org/10.1016/j.quascirev.2005.05.005

38. Aaby B (1976) Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. Nature 263:281–284. https://doi.org/10.1038/263281a0

39. Barber K (1981) Peat Stratigraphy and Climatic Change: A Paleoecological Test of the Theory of Cyclic Peat Bog Regeneration. Balkema, Rotterdam

40. Osvald H (1923) Die vegetation des Hochmoores Komosse. Sven Vaxttsociologiska Sallskapets Handl 1:1–436

41. Barber K, Langdon PG (2007) What drives the peat-based palaeoclimate record? A critical test using multi-proxy climate records from northern Britain. Quat Sci Rev 26:3318–3327. https://doi.org/10.1016/j.quascirev.2007.09.011

42. Walker D, Walker PM (1961) Stratigraphic Evidence of Regeneration in Some Irish Bogs. J Ecol 49:169–185. https://doi.org/10.2307/2257432

43. Barber KE (1993) Peatlands as scientific archives of past biodiversity. Biodivers Conserv 2:474–489

44. Niinemets E, Pensa M, Charman DJ (2011) Analysis of fossil testate amoebae in Selisoo Bog, Estonia: local variability and implications for palaeoecological reconstructions in peatlands. Boreas 40:367–378. https://doi.org/10.1111/j.1502-3885.2010.00188.x

45. Charman DJ (2007) Summer water deficit variability controls on peatland water-table changes: implications for Holocene palaeoclimate reconstructions. The Holocene 17:217–227. https://doi.org/10.1177/0959683607075836

46. Charman DJ, Brown AD, Hendon D, Karofeld E (2004) Testing the relationship between Holocene peatland palaeoclimate reconstructions and instrumental data at two European sites. Quat Sci Rev 23:137–143. https://doi.org/10.1016/j.quascirev.2003.10.006

47. Troels-Smith J (1955) Karakterisering af lose jordarter. Characterization of unconsolidated sediments. Geol Surv Den 3:1–73

48. Appleby PG (2002) Chronostratigraphic Techniques in Recent Sediments. In: Last WM, Smol JP (eds) Tracking Environmental Change Using Lake Sediments. Springer Netherlands, pp 171–203

49. Le Roux G, Marshall WA (2011) Constructing recent peat accumulation chronologies using atmospheric fall-out radionuclides. Mires Peat 7:1–14

50. Appleby PG, Oldfield F (1978) The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210Pb to the sediment. CATENA 5:1–8. https://doi.org/10.1016/S0341-8162(78)80002-2

51. Charman DJ, Hendon D, Woodland WA (2000) The identification of Testate amoebae (Protozoa:Rhizopoda) in peats. Quaternary Research Association, London

52. Amesbury MJ, Swindles GT, Bobrov A, et al (2016) Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. Quat Sci Rev 152:132–151. https://doi.org/10.1016/j.quascirev.2016.09.024

53. Duckert C, Blandenier Q, Kupferschmid FAL, et al (2018) En garde! Redefinition of Nebela militaris (Arcellinida, Hyalospheniidae) and erection of Alabasta gen. nov. Eur J Protistol 66:156–165. https://doi.org/10.1016/j.ejop.2018.08.005

54. Line JM, Ter Braak CJF, Birks HJB (1994) WACALIB version 3.3 - a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample specific errors of prediction. J Paleolimnol 10:147–152

55. Hill MO (1979) DECORANA - A FORTRAN program for Detrended Correspondence Analysis and Reciprocal Averaging. Cornell University, Ithaca, New York

56. Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Palaeontological Statistics software package for education and data analysis. Palaeontol Electron 4:9

57. Klein Tank AMG, Wijngaard JB, Können GP, et al (2002) Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. Int J Climatol 22:1441–1453. https://doi.org/10.1002/joc.773

58. Belyea LR, Clymo RS (2001) Feedback control of the rate of peat formation. Proc R Soc B Biol Sci 268:1315–1321. https://doi.org/10.1098/rspb.2001.1665

59. Monna F, van Oort F, Hubert P, et al (2009) Modeling of 137Cs migration in soils using an 80-year soil archive: role of fertilizers and agricultural amendments. J Environ Radioact 100:9–16. https://doi.org/10.1016/j.jenvrad.2008.09.009

60. Krishnaswamy S, Lal D, Martin JM, Meybeck M (1971) Geochronology of lake sediments. Earth Planet Sci Lett 11:407–414. https://doi.org/10.1016/0012-821X(71)90202-0

61. Payne RJ, Mitchell EAD (2008) How many is enough? Determining optimal count totals for ecological and palaeoecological studies of testate amoebae. J Paleolimnol 42:483–495. https://doi.org/10.1007/s10933-008-9299-y

62. Magurran AE (1988) Ecological Diversity and Its Measurement. Princeton University Press, Princeton

63. Turner TE, Swindles GT, Charman DJ, Blundell A (2013) Comparing regional and supra-regional transfer functions for palaeohydrological reconstruction from Holocene peatlands. Palaeogeogr Palaeoclimatol Palaeoecol 369:395–408. https://doi.org/10.1016/j.palaeo.2012.11.005

64. Whittle A, Amesbury MJ, Charman DJ, et al (2019) Salt-Enrichment Impact on Biomass Production in a Natural Population of Peatland Dwelling Arcellinida and Euglyphida (Testate Amoebae). Microb Ecol 78:534–538. https://doi.org/10.1007/s00248-018-1296-8

65. Patterson RT, Kumar A (2002) A review of current testate rhizopod (thecamoebian) research in Canada. Palaeogeogr Palaeoclimatol Palaeoecol 180:225–251

66. Marcisz K, Lamentowicz Ł, Słowińska S, et al (2014) Seasonal changes in Sphagnum peatland testate amoeba communities along a hydrological gradient. Eur J Protistol 50:445–455. https://doi.org/10.1016/j.ejop.2014.07.001

67. Booth RK (2008) Testate amoebae as proxies for mean annual water-table depth in Sphagnum-dominated peatlands of North America. J Quat Sci 23:43–57. https://doi.org/10.1002/jqs.1114

68. Barber K (1994) Deriving Holocene palaeoclimates from peat stratigraphy: some misconceptions regarding sensitivity and continuity of the record. Quat Newsl 72:1–9

69. Barber K, Dumayne-Peaty L, Hughes P, et al (1998) Replicability and variability of the recent macrofossil and proxy-climate record from raised bogs: field stratigraphy and macrofossil data from Bolton Fell Moss and Walton Moss, Cumbria, England. J Quat Sci 13:515–528. https://doi.org/10.1002/(SICI)1099-1417(1998110)13:6<515::AID-JQS393>3.0.CO;2-S

70. De Vleeschouwer F, Chambers FM, Swindles GT (2010) Coring and sub-sampling of peatlands for palaeoenvironmental research. Mires Peat 7:1–10

71. Väliranta M, Blundell A, Charman DJ, et al (2012) Reconstructing peatland water tables using transfer functions for plant macrofossils and testate amoebae: A methodological comparison. Quat Int 268:34–43. https://doi.org/10.1016/j.quaint.2011.05.024

72. Mauquoy D, Hughes PDM, van Geel B (2010) A protocol for plant macrofossil analysis of peat deposits. Mires Peat 7:1–5

73. Plunkett G (2006) Tephra-linked peat humification records from Irish ombrotrophic bogs question nature of solar forcing at 850 cal. yr BC. J Quat Sci 21:9–16. https://doi.org/10.1002/jqs.951

74. Payne RJ, Blackford JJ (2008) Peat humification and climate change: a multi-site comparison from mires in south-east Alaska. Mires Peat 3:1–11

75. Barber KE, Charman DJ (2003) Holocene palaeoclimate records from peatlands. In: Mackay A, Battarbee RW, Birks J, Oldfield F (eds) Global Change in the Holocene. Arnold, London, pp 210–226

76. Charman DJ (2002) Peatlands and environmental change. J. Wiley, Chichester

77. Charman DJ (2001) Biostratigraphic and palaeoenvironmental applications of testate amoebae. Quat Sci Rev 20:1753–1764. https://doi.org/10.1016/S0277-3791(01)00036-1

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)

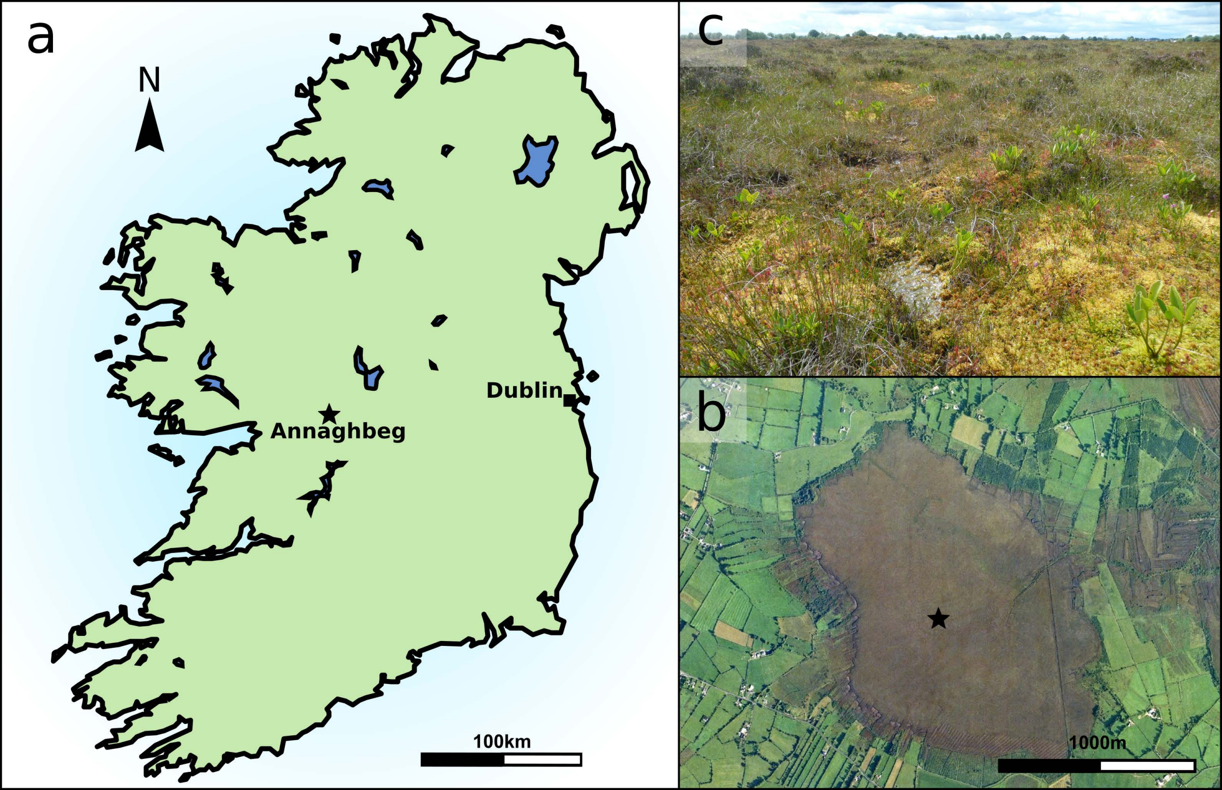
Fig. 3 a: age-depth models for the three short cores from Annaghbeg. Solid line = hummock; dotted line = lawn; dashed line = hollow. b: ^{137}Cs inventories plotted against depth in cm

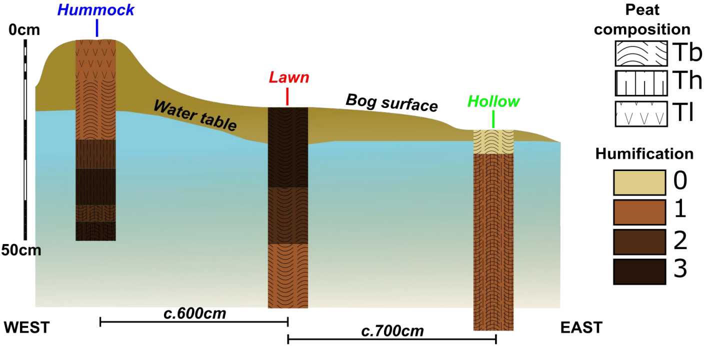
Fig. 4 Diagrams showing relative abundance of testate amoebae, expressed as percentages, from the three short cores from Annaghbeg; a: hummock; b: lawn; c: hollow. Reconstructed DWT values were generated using the Amesbury *et al.* [52] transfer function, with sample specific errors generated using 1000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

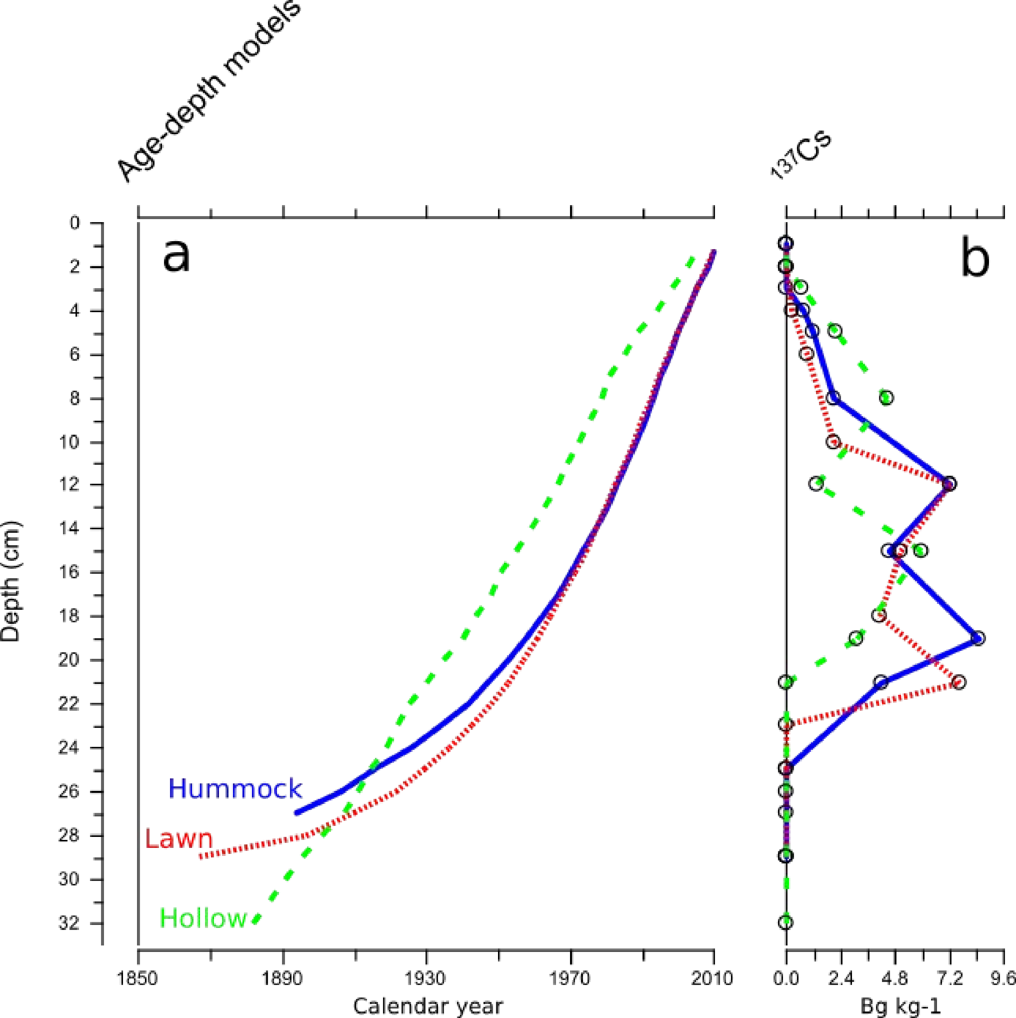
Fig. 5 Detrended correspondence analysis (DCA), 26 segments. a: taxa ordination, see Table 1 for abbreviations. b: sample ordination, each sample representing a 1 cm thick slice of core

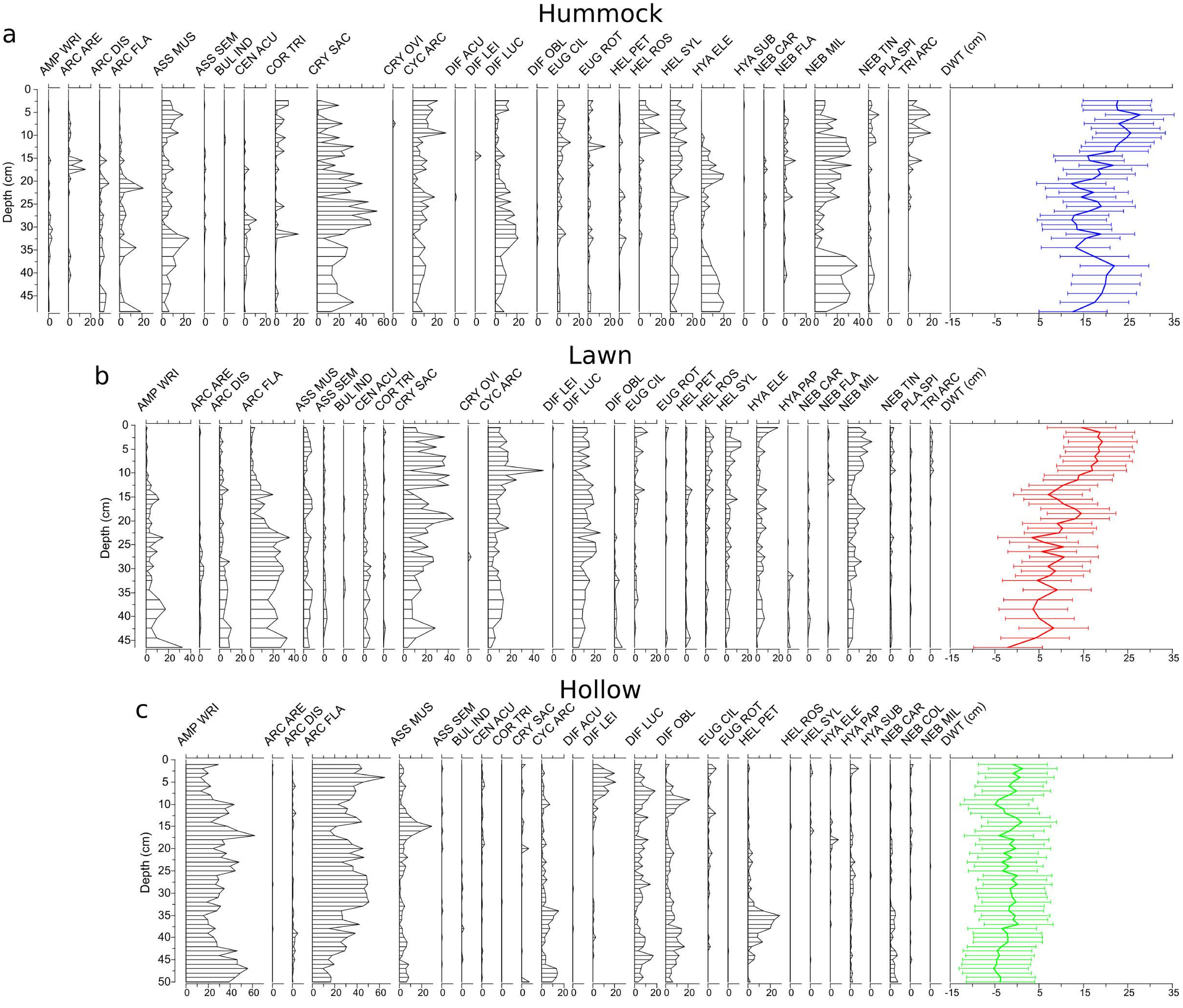
Fig. 6 Shannon-Wiener diversity indices (H') plotted against calendar year. Error bars indicate bootstrapped upper and lower estimates (999 bootstrap cycles)

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).


a
N
Dublin
Annaghbeg
100km
c
b
1000m


Hummock
0cm
50cm
Lawn
Water table
Bog surface
Hollow
Peat composition
Tb
Th
Tl
Humification
0
1
2
3
c.600cm
c.700cm
WEST
EAST


Age-depth models
137Cs
a
b
Depth (cm)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
Hummock
Lawn
Hollow
1850
1890
1930
1970
2010
Calendar year
0.0
2.4
4.8
7.2
9.6
Bg kg-1


Hummock
a
AMP WRI
ARC ARE
ARC DIS
ARC FLA
ASS MUS
ASS SEM
BUL IND
CEN ACU
COR TRI
CRY SAC
CRY OVI
CYC ARC
DIF ACU
DIF LEI
DIF LUC
DIF OBL
EUG CIL
EUG ROT
HEL PET
HEL ROS
HEL SYL
HYA ELE
HYA SUB
NEB CAR
NEB FLA
NEB MIL
NEB TIN
PLA SPI
TRI ARC
DWT (cm)
Depth (cm)
0
5
10
15
20
25
30
35
40
45
-15
-5
5
15
25
35
Lawn
b
AMP WRI
ARC ARE
ARC DIS
ARC FLA
ASS MUS
ASS SEM
BUL IND
CEN ACU
COR TRI
CRY SAC
CRY OVI
CYC ARC
DIF LEI
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EUG CIL
EUG ROT
HEL PET
HEL ROS
HEL SYL
HYA ELE
HYA PAP
NEB CAR
NEB FLA
NEB MIL
NEB TIN
PLA SPI
TRI ARC
DWT (cm)
Depth (cm)
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COR TRI
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DIF LUC
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EUG CIL
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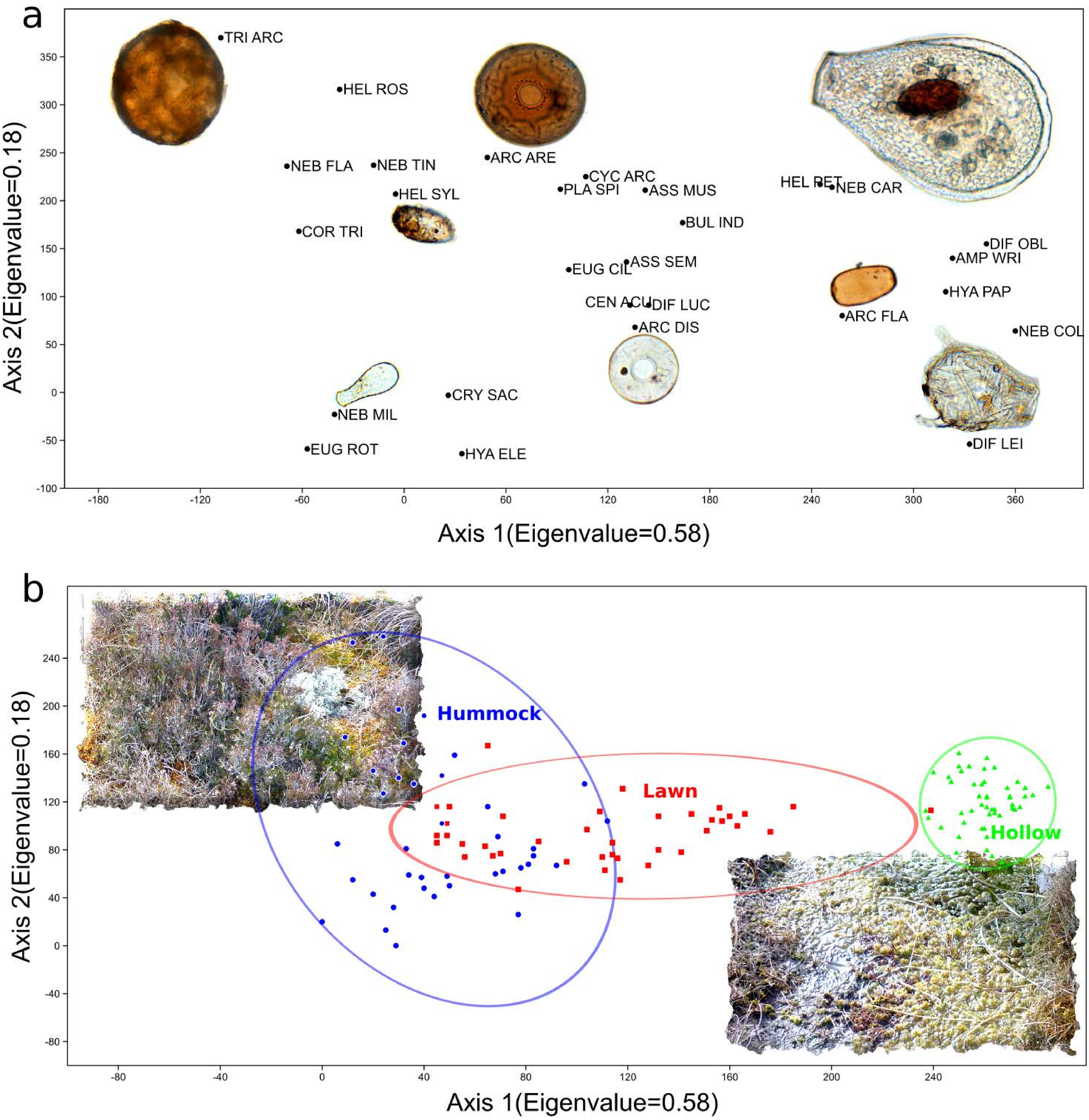
HEL PET
HEL ROS
HEL SYL
HYA ELE
HYA PAP
HYA SUB
NEB CAR
NEB COL
NEB MIL
DWT (cm)
Depth (cm)
50
0
20
40
60


a
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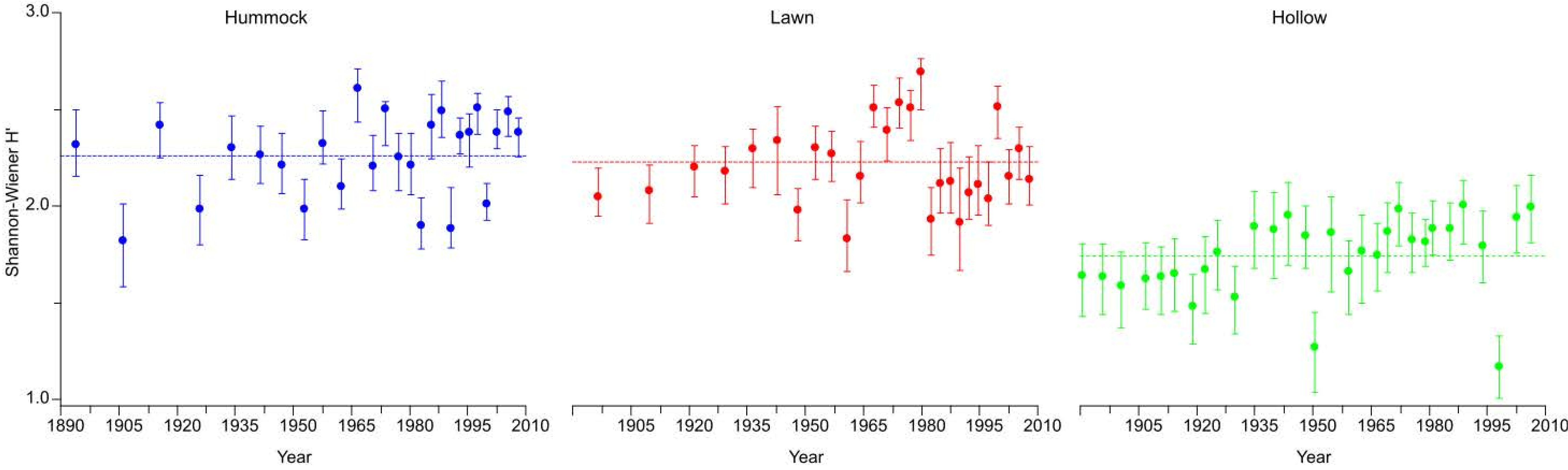
HYA PAP
ASS SEM
EUG CIL
CEN ACU
DIF LUC
ARC DIS
ARC FLA
NEB COL
CRY SAC
NEB MIL
EUG ROT
HYA ELE
DIF LEI
Axis 2(Eigenvalue=0.18)
350
300
250
200
150
100
50
0
-50
-100
-180
-120
-60
0
60
120
180
240
300
360
Axis 1(Eigenvalue=0.58)
b
Hummock
Lawn
Hollow
Axis 2(Eigenvalue=0.18)
240
200
160
120
80
40
0
-40
-80
-80
-40
0
40
80
120
160
200
240
Axis 1(Eigenvalue=0.58)


Hummock
Lawn
Hollow
Shannon-Wiener H'
3.0
2.0
1.0
1890
1905
1920
1935
1950
1965
1980
1995
2010
Year
1905
1920
1935
1950
1965
1980
1995
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Year
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1920
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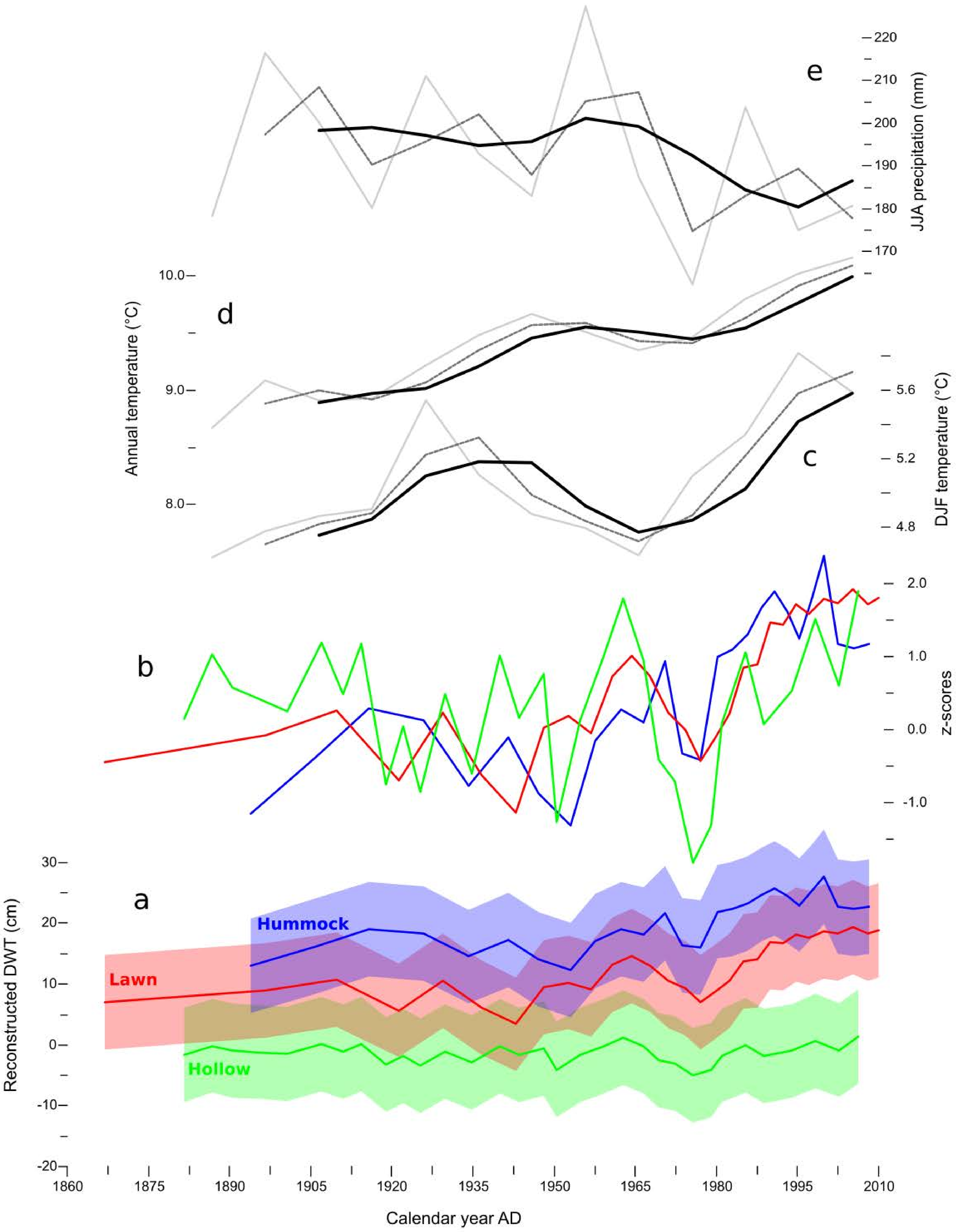
1965
1980
1995
2010
Year


e
JJA precipitation (mm)
220
210
200
190
180
170
d
Annual temperature (°C)
10.0
9.0
8.0
c
DJF temperature (°C)
5.6
5.2
4.8
b
z-scores
2.0
1.0
0.0
-1.0
a
Hummock
Lawn
Hollow
Reconstructed DWT (cm)
30
20
10
0
-10
-20
1860
1875
1890
1905
1920
1935
1950
1965
1980
1995
2010
Calendar year AD