LETTER

Low-salinity transitions drive abrupt microbial response to sea-level change

Alex Whittle[1,2] | Robert L. Barnett[1,3] | Dan J. Charman[1] | Angela V. Gallego-Sala[1]

[1]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK

[2]British Antarctic Survey, Natural Environment Research Council, Cambridge, UK

[3]Département de biologie, chimie et géographie et Centre d'études nordiques, Université du Québec à Rimouski, Rimouski, Canada

Correspondence
Alex Whittle and Robert L. Barnett, Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK.
Email: aw424@exeter.ac.uk; r.barnett@exeter.ac.uk

Abstract

The salinisation of many coastal ecosystems is underway and is expected to continue into the future because of sea-level rise and storm intensification brought about by the changing climate. However, the response of soil microbes to increasing salinity conditions within coastal environments is poorly understood, despite their importance for nutrient cascading, carbon sequestration and wider ecosystem functioning. Here, we demonstrate deterioration in the productivity of a top-tier microbial group (testate amoebae) with increasing coastal salinity, which we show to be consistent across phylogenetic groups, salinity gradients, environment types and latitude. Our results show that microbial changes occur in the very early stages of marine inundation, presaging more radical changes in soil and ecosystem function and providing an early warning of coastal salinisation that could be used to improve coastal planning and adaptation.

KEYWORDS
biomass, climate change, coastal ecology, microbial, productivity, salinity, sea level, testate amoebae

INTRODUCTION

Increasing rates of sea-level rise, frequency of extreme sea-level events and intensification of cyclone activity (IPCC 2019) during the present century are driving changes to coastal environments worldwide; contributing to the submergence of low-lying islands (Storlazzi et al., 2018), increased coastal flooding (Vitousek, 2017), contamination of groundwater (Taylor et al., 2013) and significant changes to coastal wetlands (Schuerch et al., 2018). As salt-water encroaches, sodium chloride and other salts (such as sulphates) are deposited further inland, increasing ionic concentrations and altering redox conditions (Jansson et al., 2020). Coastal soil ecosystems that have previously been dominated by freshwater are especially vulnerable to such salt-enrichment because few of the organisms they contain possess suitable physiological adaptions to thrive under more saline conditions. While studies of salt-stressed soil communities remain scarce, salinisation has been shown to drive ecosystem changes ranging from negative and deleterious effects on individual microbial (Roe & Patterson, 2014), plant and invertebrate communities (Pereira et al., 2018) to wholesale ecosystem reorganisations, such as the formation of ghost forests on submerging coasts of North America (Kirwan et al., 2019).

Salinisation-driven changes in the microbial productivity of coastal soils is both pertinent to future greenhouse gas production and carbon cycling (Pereira et al., 2018) and may also serve as an early indicator of impending 'state-shift' ecosystem change. Yet crucially, beyond shifting patterns in the species composition of communities, understanding of microbial community-level responses to salinisation remains elusive, especially in terms of productivity.

Initial measurements of prokaryotic biomass in soils exposed to high salt-enrichment levels have indicated strong (albeit apparently inconsistent) responses, which differ by community and environment type (Pereira et al., 2018), and in spite of the narrow salt-tolerances described for many eukaryotic lineages, comparable quantifications of productivity are lacking. Understanding how microbial productivity responds to changes in coastal salinity gradients, prior to and during inundation, will be critical for informing predictions of ecosystem evolution and greenhouse gas fluxes in coastal soils, as well as for supporting resilience strategies within environmental change biology.

Here we use testate amoebae (TA) to evaluate the hypothesis that heterotrophic eukaryote productivity in fresh- and brackish-water coastal soils responds to low-magnitude increases in salt exposure. To represent the conditions that occur early within marine-transgressions we define low-magnitude increases as less than 10% of seawater salinity level. TA provide a model system as they occupy the highest levels of microbial food webs throughout almost all freshwater and brackish ecosystems on Earth (Dumack et al., 2018; Geisen et al., 2018; Jassey et al., 2013) and represent a considerable component of soil-microbial nutrient and carbon cascading (Potapov et al., 2019). Crucially, they produce decay-resistant shells (termed tests), which has led to their widespread establishment as a bio-indicator for monitoring ecosystem health (Karimi et al., 2016) and past environmental conditions (Mitchell et al., 2008) and permits highly precise determination of changes in their productivity through time.

We drew together records of natural TA communities present within overlapping salinity gradients from coastal environments exposed to differing salt deposition regimes (salt marsh, brackish marsh and coastal peatland). Together, these gradients represent salinity conditions spanning from predominantly freshwater to diurnal tidal inundation (Figure 1a). Samples avoided potentially confounding effects from anthropogenic activity and originated from geographically diverse but climatically similar locations on Marion Island (sub-Antarctica) and the Magdalen Islands (Canada) – average air temperature 2005–2010, 5.6℃ and 5.9℃ respectively (Colwell, 2002; Lawrimore et al., 2016).

We identify a highly significant and consistent decline in TA productivity due to the salinisation of coastal environments, which is consistent across TA lineages, environment types and through time. The rapid response of this model organism to salinisation advocates for their use as bioindicators of Earth monitoring systems and for wider studies on coastal ecosystem functioning in response to sea-level rise.

MATERIAL AND METHODS

Data collation and taxonomic harmonisation

We compiled records of natural soil-dwelling TA communities representative of different coastal environments from published literature. To be accepted for analysis, we required that TA community data (i.e., relative abundance calculated from census counts) had constrained total concentrations (i.e., tests per unit volume of sediment), and also paired environmental conductivity estimates (μS) from the precise sampling locations. These measurements were used to provide approximations of productivity and salinity respectively. This data search yielded 85 samples from four distinct transects of variable coastal salt deposition at three independent coastal environment sites. The dataset comprised 31 samples from two transects across a salt marsh in the Magdalen Islands, Canada (47.4°N, 61.9°W) (Barnett et al., 2017a); 26 samples from one transect across a brackish, tidal marsh also in the Magdalen Islands (Barnett et al., 2017a) and 28 samples from one transect across a sub-Antarctic coastal peatland on Marion Island (46.9°S, 37.6°E) (Whittle et al., 2019). Full site descriptions are available in the original sources. Although the dataset used in this study represents the higher latitudes of both hemispheres, the current unavailability of samples from a wider range of latitudes identified by the data search is recognised by the study.

Original taxonomic designations (presented in Whittle et al., 2019 and Barnett et al., 2017a) were updated and harmonised to ensure that included taxa were consistent and closely representative of biological species (Extended Data Table S3). Specifically, we combined *Phryganella acropodia* and *Difflugia globulosa* (maintaining the designation of *P. acropodia*) because separation requires observation of living-cells which were not differentiated during creation of the records; *Cyclopyxis* spp. (in Whittle et al., 2019) was re-designated as *C. eurystoma*, and *Corythion dubium* (in Whittle et al., 2019) was merged with *Corythion-Trinema* type.

Calculation of surface productivity and biomass

Within the original studies, communities of TA were enumerated from samples of denuded surface sediment (defined as the topmost 1-cm layer), which were hermetically stored after collection. TA were isolated from the sediment matrix following the standard water-based protocol for peat-soils provided in Charman et al. (2000), however modifications suitable for salt-marsh sediments (after Barnett et al., 2013) were applied for samples from the Canadian sites. Identification was conducted directly by light-microscope at x200–400 magnification and was based on morphological features of the tests (composition, shape, ornamentation, size and colour). Census counts of each sample included all individuals (i.e. living and encysted cells and empty tests) to minimise bias in assemblages caused by seasonal blooms (Barnett et al., 2013). Taxonomy primarily followed Charman et al. (2000), although supplementary references were used for the identification of regional and environment specific taxa (Barnett et el., 2016, 2017a,b; Whittle et al., 2019).
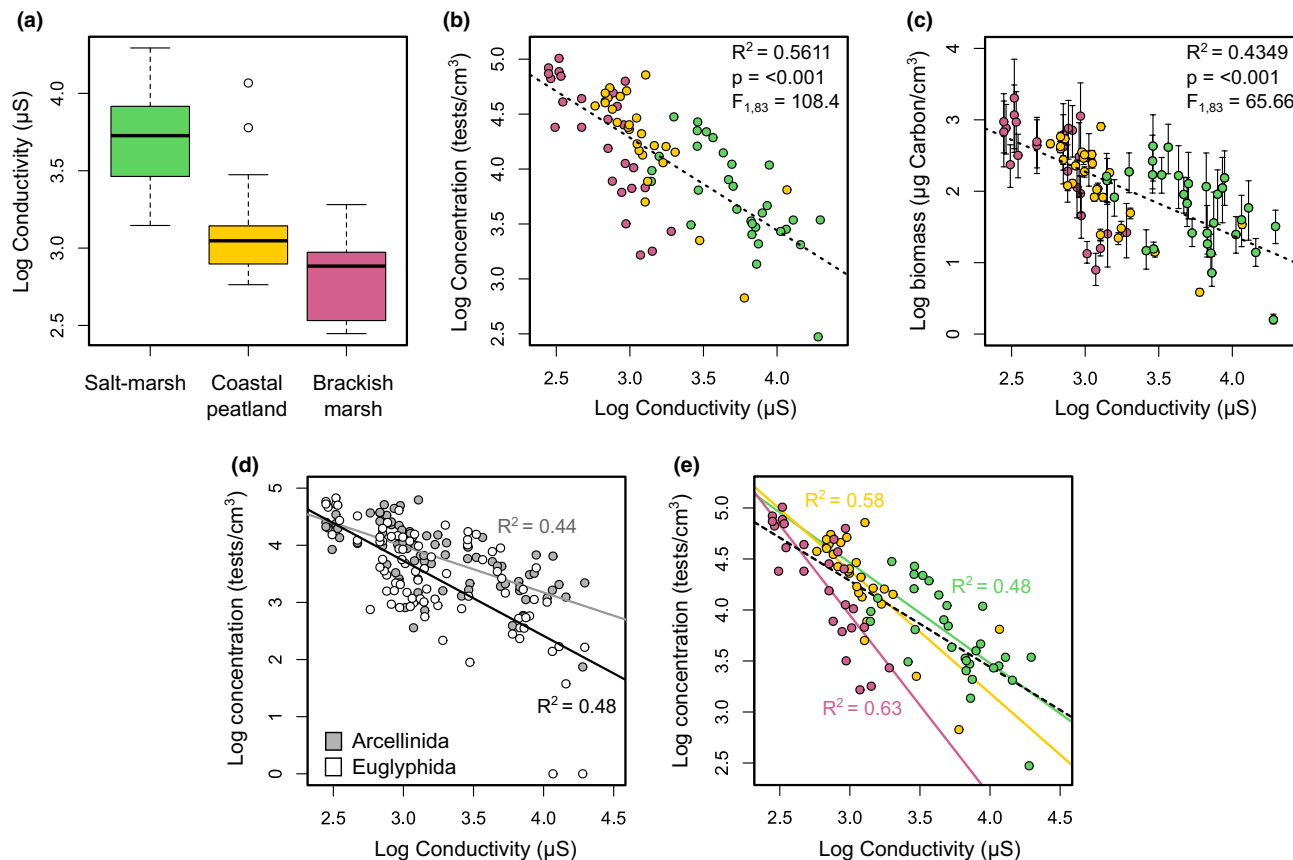
FIGURE 1 Salinity conditions and testate amoebae community response along salt-enriched environmental gradients. (a) ranges of conductivity (used here as a proxy for salinity) across sampled environmental types, and (b) the response of testate amoebae concentrations (used here as a proxy for productivity), as well as the response of community biomass (c), along these gradients. Error bars represent uncertainty resulting from ranges in the size of individual taxa (see Extended Data Table S4). The total salinity gradient sampled across all three environment type spans 280–20,000 μS. Also shown are changes in productivity (viz. concentration) distinguished by the two major orders of testate amoebae (d) Arcellinida (light grey; $R^2 = 0.4369$, $F_{1,83} = 66.17$) and Euglyphida (white; $R^2 = 0.4769$, $F_{1,83} = 77.59$), both $p \leq 0.001$. Statistical difference in slope gradients tested using analysis of covariance (ANCOVA) shows that regression slopes are not homogenous between the orders ($F = 7.840$, $p \leq 0.01$). (e) Changes in productivity distinguished by environment type (colours as in panel a), all relationships significant at $p \leq 0.001$

Total test concentrations per unit sediment volume (i.e. tests cm^{-3}), estimated from the ratio of tests to parallel counts of an exotic marker of known concentration (*Lycopodium clavatum* L.; Stockmarr, 1971) were used as an approximation of productivity over time. Total TA production is a function of the accumulation of dead (empty) tests plus generation of new live tests during a given period (Schönborn, 1982, 1986; Wilkinson & Mitchell, 2010). Our test concentration data originate from the top 1 cm of surface sediment, representing a time-averaged period of ~12 years and thus many hundreds of TA generational cycles. Assuming consistent preservation, over such a time-averaged period the accumulation of dead tests would be expected to dominate the total (i.e. dead plus live) production signal, allowing our inference of productivity from test concentration to be robust. However, we recognise that calculations of true TA productivity rates require an assessment of live tests (unavailable for this study) and that population specific production varies across species (Schönborn, 1983; Wilkinson & Mitchell, 2010).

To calculate biomass, average biovolume of each taxon was calculated assuming standard geometric test shapes (Mitchell et al., 2004) and average test dimensions (Extended Data Table S4). Biovolume was converted to biomass using the factor 1 μm^3 = 1.1 × 10^{-7} μg Carbon (Mitchell et al., 2004). Total biomass of the TA community at each sampling station was quantified by multiplying these values by the concentration of each taxon. Because information relating to the ratio of live:dead individuals were unavailable in this study, we define biomass as the sum of all individuals recorded within each sample, following Mitchell (2004) and Royles et al. (2016).

Quantification of environmental salinity conditions

The salinity of each microhabitat was measured at the TA sampling stations, spaced within each transect, by

using pore-water conductivity, which is linearly related to salinity under the environmental conditions present (Wagner et al., 2006). A calibrated Hanna Instruments probe (HI98129/HI98130) was used to measure pore-water conductivity from groundwater recharge within small boreholes (Canadian sites) and from water extracted from sub-samples of surface (5 cm) material under laboratory conditions, where in situ measurements were not possible (Marion Island sites). The dominant source of oceanic salts to the brackish and saltmarsh sites is via coastal flooding and tidal inundation, whereas the coastal peatland sites receive salt solely from atmospheric deposition (i.e. wind-blown salt-spray and precipitation).

Statistical analysis of surface data

Linear regressions of log transformed surface productivity and biomass data against conductivity measurements were performed in R (version 3.6.3) (R Core Team, 2020). Detrended correspondence analysis (DCA) Axis 1 scores, calculated from relative abundance (%) data for each sampling station were used to classify the overall species response to salinity; where values >2 standard deviations suggest a unimodal response (Birks, 1995; ter Braak & Prentice, 1988; Šmilauer & Lepš, 2014). Correspondence analysis (CA) based on untransformed species relative abundance (%) data, including all observed taxa, was used to summarise variation in community composition between sampling stations. All multivariate analyses were performed in the statistical package 'vegan' (Oksanen, 2017) within R (R Core Team, 2020). Analysis of covariance (ANCOVA) was used to test the homogeneity of regression slopes (gradients) for the relationship between conductivity and TA concentrations for each of the salt-enriched environment types and was conducted using the R package 'car' (Fox et al., 2012). The Sørensen similarity index (a metric of beta-diversity) was calculated for pairs of samples as a function of the difference in their observed conductivity (using species presence-absence data) and partitioned into turnover and nestedness components using the 'betapart' package for 'R' (Baselga et al., 2017).

Reconstruction of changes in productivity through time

Sub-fossil TA communities from sediment cores collected at the salt marsh and brackish marsh environments in the Magdalen Islands (Barnett et al., 2017a) were compiled to explore TA responses to salinity changes through time. Communities were enumerated at contiguous intervals through the top ~30 cm of each core (approximately equivalent to the past 300 years). Productivity values were calculated for each interval using the method described for surface samples. Relative changes in salinity were reconstructed by standardising (using z-scores) derived conductivity values that were calculated using the relationship between TA productivity and conductivity (Figure 1b). The reconstructed salinity trend was compared against independent foraminifera-derived relative sea-level reconstructions from the same locations and sedimentological descriptions from the original study (Barnett et al., 2017a). Age-depth modelling, used to assign years of deposition and uncertainties to each 1-cm slice in the sediment cores, applied a Bayesian statistical approach (Blaauw & Christen, 2011) that combined independent radiocarbon (^{14}C) and radionuclide (^{210}Pb) dates, as described in the original study (Barnett et al., 2017a).

Statistical analysis of Palaeoenvironmental data

Identification of statistically significant changepoints within the TA derived conductivity and foraminifera inferred sea-level time-series was conducted using the cpt. meanvar function of the 'changepoint' (Killick & Eckley, 2013) R package, to find concurrent changes in the mean and variance for each time series (default settings were adopted). Pearson correlation between TA-derived conductivity and foraminifera inferred sea-level was conducted using second-order polynomial LOESS smoothed data, resampled to consistent 25 year intervals.

RESULTS

We found a highly significant (negative exponential) decline in the productivity ($R^2 = 0.5611$; $p < 0.001$; Figure 1b) and biomass ($R^2 = 0.4349$; $p < 0.001$; Figure 1c) of TA communities with increasing microhabitat salinity conditions, a response that remained consistent throughout different locations and coastal environment types. The productivity of populations from both major TA lineages also exhibited consistent trends; Arcellinida ($R^2 = 0.4369$; $p < 0.001$) and Euglyphida ($R^2 = 0.4769$; $p < 0.001$) (Figure 1d). Productivity of Euglyphid species underwent comparatively steeper decline, suggesting generally lower salt tolerance compared with species within the Arcellinida order.

This remarkably consistent relationship also indicates that the productivity of natural TA communities throughout brackish and freshwater ecosystems is highly sensitive to small perturbations in salinisation regime. For example, the modelled trajectory for the community within the lowest recorded salinity conditions suggested that an enrichment of only 357 μS (equivalent to ~0.7% of the salinity of sea water) would reduce community size by 50%, while 4000 μS (~8% sea-water equivalent) would lead to a 90% reduction (Figure 1b). Accordingly, a statistically significant and slightly shallower rate of

productivity decline was observed in communities from environments exposed to higher average salinisation levels (i.e. those inhabiting the salt marsh and coastal peatland sites) indicating comparatively greater resistance of pre-exposed communities to further salinity changes (Figure 1e; Extended Data Table S1).

Changes in the species composition of communities, derived from CA of species relative abundance data (Extended Data Figure S1), occurred in concert with increasing microhabitat salinity, indicating reorganisation throughout the salinity gradient in favour of more salt-tolerant species (Figure 2a; Extended Data Table S2). Within the coastal peatland and brackish marsh sites, values of the Sørensen similarity index (beta diversity) demonstrate that pairs of samples with greater differences in observed conductivity (salinity) generally exhibit more dissimilar assemblages (Figure 2b). Meanwhile, within the salt-marsh site, the lack of an overall trend similar to the coastal peatland and brackish marsh sites (Figure 2b), indicate that assemblages throughout the transect are comparatively homogenous. For all locations, the proportions of Sørensen similarity index values attributed to species turnover outweigh those of nestedness (Figure 2c). This suggests that the differences in species composition observed throughout the transects can be more strongly attributed to the replacement of species than simply loss of the species present in richer sites. Compositional turnover, which reflects the optima and tolerance of individual taxa (Barnett et al., 2017b; Roe & Patterson, 2014; Whittle et al., 2019), is therefore expected to be responsible for partially offsetting declining productivity as salinity levels become sub-optimal for certain species and more favourable to others. In support of this, we observed a statistically independent and steeper rate of productivity

decline when the effect of turnover was minimised by including only common species, which we define as those shared between all three environment types (Extended Data Figure S2). Nevertheless, our data highlight that despite the presence of moderately salt-tolerant species within the available pool (Extended Data Figure S3), turnover is insufficient to maintain large TA communities as salinity levels increase. This is to say, species tolerant of more saline conditions are less productive under higher-salinity conditions than their freshwater counterparts are under very low-salinity conditions.

Although our use of TA as a model organism does not represent the entire microbial community, we show that the effective removal of this important group of heterotrophic microbial-eukaryotes from the coastal soil microbiome is initiated following even very low levels of salt enrichment. This emphasises the potential risk that coastal salinisation poses to broader soil microbial functioning, strongly indicating that changes in microbial productivity are likely to occur early within salt-stress-induced ecosystem transitions (e.g. increased frequency coastal flooding events).

To test this hypothesis we examined the response of TA communities to historical changes in salinisation. We used co-located but independently derived sea-level reconstructions (Barnett et al., 2017a) from the salt-marsh and brackish-marsh sites included in this study to compare local sea-level changes against salinity derived from trends in sub-fossil TA productivity. Both sequences chart an ecosystem evolution with a clear trend towards higher salinity regimes (i.e. rising sea level) and are punctuated with spatially and temporally consistent 'state-shift' events (e.g. the transition from high- to mid-marsh conditions). Directional trends in salinity interpreted from the productivity of sub-fossil TA
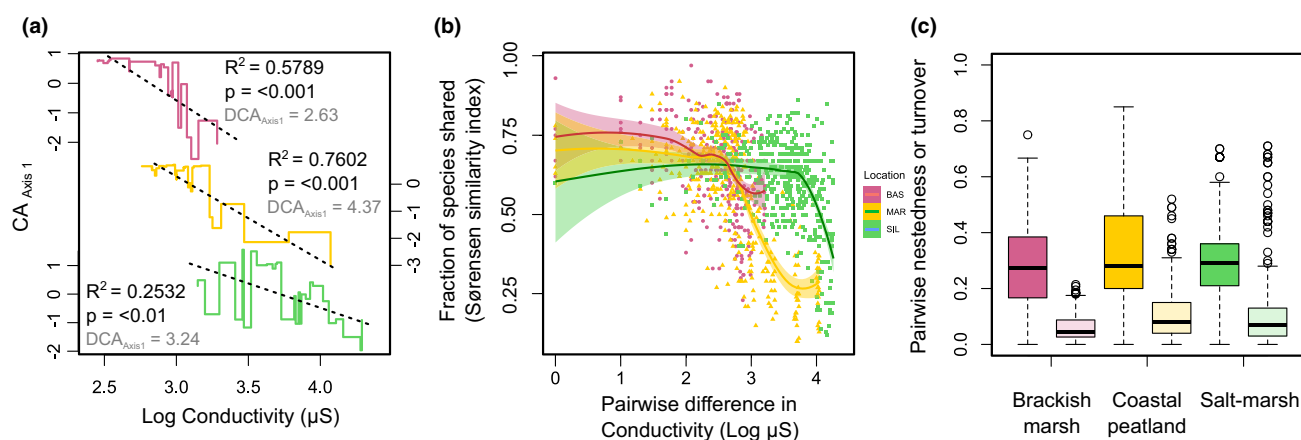

FIGURE 2 Response of community compositions along sampled salinity gradients. (a) Correspondence analysis (CA) Axis 1 scores for each sampling station provides an indication of the extent of species turnover, where similar values indicate more similar species composition of assemblages. Also shown are detrended correspondence analysis (DCA) scores for each environment type in standard deviation units, indicating overall species response to salinity is unimodal for all environment types. (b) Sørensen similarity index between pairs of samples as a function of the difference in observed conductivity (salinity) conditions. Lines for each environment type represent LOESS-smoothing. (c) Values for the pairwise turnover (darker shading) and nestedness (lighter shading) components of beta-diversity for each environment type. Colours in all panels correspond with Figure 1a (brackish marsh, red; coastal peatland, yellow; salt-marsh, green)

communities occur synchronously with these recorded changes (Figure 3; Extended Data Figure S4), and statistical changepoints within the resultant time-series show coherent timings with the significant environmental
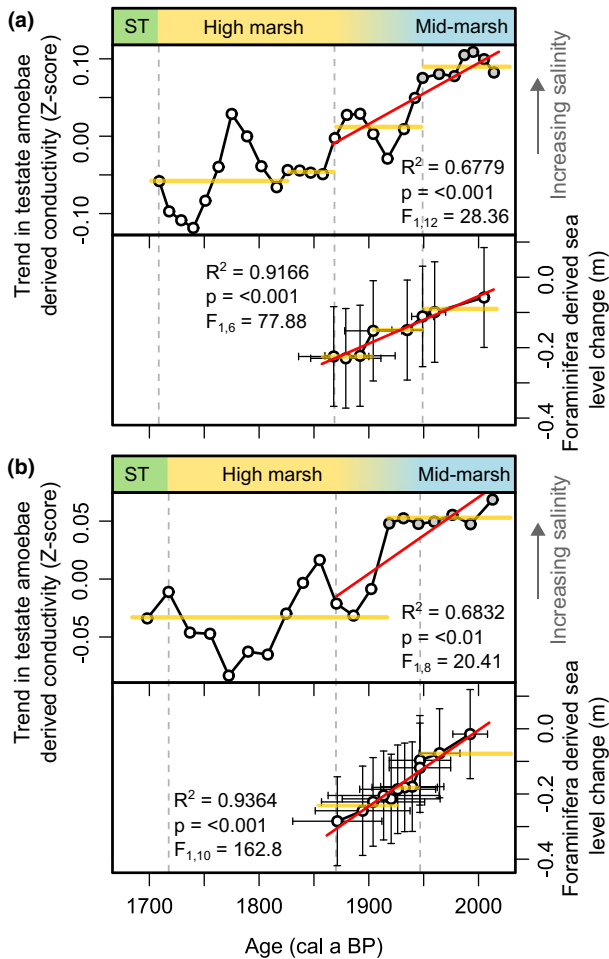

FIGURE 3 Response of testate amoebae (TA) community size to ecosystem state-shifts induced by past sea-level change in brackish marsh (a) and salt-marsh (b) environments. TA-derived conductivity reconstructions (top panels) calculated by applying the salinity relationship (Figure 1b) to sub-fossil TA community sizes (concentration). Sea-level reconstructions (bottom panels) are calculated from foraminifera-derived transfer function model predicted marsh surface elevations (Barnett et al., 2017a) and both reconstructions apply age-depth models from the original study (Barnett et al., 2017a) for temporal constraints. Environmental transitions (top shaded bars) are based on sedimentological and biostratigraphical interpretations of the sediment-core data and are independent from TA communities. In both records, the conversion from supratidal (ST; green) to intertidal occurs with the first tidal submergence around 1710 CE, with high-marsh (yellow) conditions persisting until ~1870 CE when the transition towards mid-marsh (blue) begins. The present-day, mid-marsh state of both ecosystems is reached by ~1950 CE. Red lines indicate linear regressions over time-spans equivalent to the length of the sea-level reconstructions. Yellow lines indicate statistically derived change points in the reconstructed trends. Pearson correlation coefficients reflect the correlation between TA-derived conductivity and Foraminifera sea-level estimates for each environment. Untransformed TA concentration profiles from both cores are presented in Extended Data Figure S5

state-shifts defined from independent indicators, such as foraminifera assemblages and sedimentology (Figure 3). Taken together, the consistent timings and direction of the TA response to rising sea levels confirms that communities respond sensitively and rapidly to these environmental transitions. Combined with the low-levels of salinity observed to initiate these changes, our data show that TA can serve as early indicators of future ecosystem evolution in response to salinisation, with great potential to detect environmental perturbations (Trevathan-Tackett et al., 2019) and support Earth monitoring systems (Ranasinghe, 2020; Ward et al., 2020).

DISCUSSION

The cause of productivity decline under higher salinity regimes remains unclear from our field-based study. However, we suggest that the remarkable consistency of the relationship throughout differing environments, varying species assemblages, and time, points towards an intrinsic physiological property shared among many TA species. Although salt-tolerant species are known to occur (Barnett et al., 2017b), TA are most abundant and diverse in predominantly water-logged freshwater environments, including ombrotrophic peatlands where ionic concentrations can be extremely low. High concentrations of solute ions are, therefore, likely to initiate amoebic osmoregulation mechanisms in order to balance osmotic pressure across cell membranes and prevent (or at least delay) cytolysis. Nevertheless, high salinity conditions do not necessarily cause cell mortality. Experimental exposure of Euglyphid TA to hyperosmotic stress indicates that certain species can withstand temporary stress by forming dormant pre-cysts, albeit at the cost of reproductive function and, therefore, a reduced rate of productivity (Wanner et al., 2020). Both pre-cyst formation and the subsequent recovery (assuming conditions quickly return to more optimal salinity levels) occurs very rapidly (Wanner et al., 2020) meaning that changes in community size through time more strongly reflect longer-term or average salinity conditions than 'one-off' short-lived events, such as salt-spray deposition from the atmosphere during an individual storm.

Indirect impacts are also expected to contribute to declining productivity levels. As predominantly high trophic level microbial-consumers (Dumack et al., 2018; Jassey et al., 2013), TA are also vulnerable to underlying changes in resource availability; specifically the presence of, and competition for, the lower order microbial populations that partially comprise their prey. Reduced growth rates and shifts in species composition of prey organisms (e.g. soil fungi and bacterial communities) and the expansion of foraminifera populations, which are seen to occupy an overlapping niche with TA (e.g. Kemp et al., 2017) and may compete for resources, have been observed

in response to salinisation (Rath et al., 2019; Wanner et al., 2020). Importantly, such changes in microbial predator-prey mass ratios as a result of environmental stress have wider implications for total microbial activity across trophic levels (Reczuga et al., 2018), nutrient cycling, including carbon (Jassey et al., 2015), nitrogen (Geisen et al., 2018) and silica (Wanner et al., 2020), and plant functioning (Gao et al., 2019). As a key microbial group in soil ecosystems (Gao et al., 2019; Geisen et al., 2017), the effects of salinisation on TA, whether directly or indirectly driven, will therefore play an important role in determining food web structures, nutrient cascading and carbon budgets at the coast.

This study set out to define a first-order relationship between salinity and communities of TA in coastal brackish and freshwater systems. The striking consistency of the relationship we observed across different coastal environments and through time indicates substantial applications of TA for (1) forecasting the microbial response to future coastal salinisation under different scenarios (e.g. from salt-spray aerosol deposition through to complete inundation) and (2) providing a novel tool to derive records of past salinity changes from coastal sediments, useful for palaeoenvironmental analysis (e.g. in developing reconstructions of sea-level and wind-driven salt-spray deposition) and for informing coastal management decisions. Considering that TA are representative microbial eukaryotes, top-tier microbial heterotrophs and drivers of microecological ecosystem functioning, the sensitivity we observe potentially alludes to the vulnerability of the wider microbiome of coastal soils to low-level salinisation, not considered by previous research efforts.

Our study does not extend to wider ecosystem functioning because the necessary covariate data (e.g. plant composition, soil and water properties and predator/prey ratios) were not available for inclusion within the data compilation. However, the potential importance of a wide range of variables beyond salinity should not be overlooked. For example, soil moisture, pH and temperature variability have all been identified as critical variables that control TA density and diversity in non-coastal environments (Geisen et al., 2018 and references therein). Although the observed decline in TA productivity and biomass in response to salinisation appears (at least initially) an environmental concern, it is not yet clear whether the close interactions between soil protist groups and plants (Gao et al., 2019) provide functional redundancy, or whether the TA response to salinity is an indication of wider ecosystem functioning exposure. Further research is now needed to better understand the context of this response within wider ecosystem changes and to quantify the impact of entire community changeover (i.e. towards fully halophytic taxa across trophic levels) on nutrient availability for plant functioning and carbon cycling for sequestration potential.

AUTHOR CONTRIBUTION

All authors conceptualised the study. AW and RLB led on data curation and methodological design. AW led on formal analysis and visualisation with support from RLB. RLB led on the original manuscript draft with support from AW. All authors reviewed and edited the manuscript. DJC and AGS provided project supervision and funding acquisition.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13893.

DATA AVAILABILITY STATEMENT

Authors have data permissions for all data used in this study. Data deriving from published sources are referenced in the manuscript. The datasets used in this study are available from the British Antarctic Survey Polar Data Centre, and the figshare repository (https://doi.org/10.6084/m9.figshare.16573346.v1).

ORCID

Alex Whittle https://orcid.org/0000-0001-9615-7579
Robert L. Barnett https://orcid.org/0000-0001-6179-8456
Angela V. Gallego-Sala https://orcid.org/0000-0002-7483-7773

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