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High risk of extinction of benthic foraminifera in this century due to ocean acidification

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Increased atmospheric CO_2 concentrations lead to decreased pH and carbonate availability in the ocean (Ocean Acidification, OA). Carbon dioxide seeps serve as 'windows into the future' to study the ability of marine invertebrates to acclimatise to OA. We studied benthic foraminifera in sediments from shallow volcanic CO_2 seeps in Papua New Guinea. Conditions follow a gradient from present day pH/pCO$_2$ to those expected past 2100. We show that foraminiferal densities and diversity declined steeply with increasing pCO$_2$. Foraminifera were almost absent at sites with pH < 7.9 (>700 µatm pCO$_2$). Symbiont-bearing species did not exhibit reduced vulnerability to extinction at <7.9 pH. Non-calcifying taxa declined less steeply along pCO$_2$ gradients, but were also absent in samples at pH < 7.9. Data suggest the possibility of an OA induced ecological extinction of shallow tropical benthic foraminifera by 2100; similar to extinctions observed in the geological past.

A tmospheric carbon dioxide (CO_2) concentrations are nearly 40% above pre-industrial levels, and are likely to double by the end of this century[1]. The absorption of atmospheric carbon dioxide by the oceans decreases pH and carbonate availability[2] ('ocean acidification', OA). These changes can have deleterious effects on marine invertebrates relying on calcification[3,4]. Volcanic carbon dioxide seeps[5,6] can provide proxies to investigate how calcifying marine organisms acclimatise to exposure to OA. Recent studies of CO_2 seeps in shallow temperate and tropical marine ecosystems provided the first data on ecosystem-wide changes caused by OA. These studies documented negative effects of OA on calcifying organisms including corals, echinoderms, gastropods, crustose coralline algae and foraminifera[5–8]. In contrast, seagrasses, microalgae or non-calcifying macroalgae either benefitted from increased DIC availability or were resilient to pH/DIC changes[5–10]. At the tropical seeps, coral diversity and structural complexity sharply dropped as pCO$_2$ values approached those expected for the end of this century, while coral cover remained unaffected[5].

Benthic foraminifera are a diverse group of large protists (up to 2 cm) that have an organic wall, form carbonate tests though biotic calcification or form tests through agglutination of sediment particles. Tropical foraminifera have high calcification rates and are important contributors to carbonate sediments. The tests of calcifying foraminifera are made of either high- or low magnesium calcite (Mg-calcite), while only a few taxa produce aragonite[11]. High Mg-calcite is the most soluble form of carbonate, and organisms producing high-Mg-calcite are considered particularly vulnerable to OA.

Many tropical foraminiferal taxa live in symbiosis with unicellular dinoflagellates, diatoms, green or red algae or retaining chloroplasts from algal food and are thus mixotrophic, while the remainder are predominantly heterotrophic. Several studies have investigated the effects of OA on benthic foraminifera. Experiments using CO_2 to manipulate seawater chemistry on four species of diatom-bearing and two dinoflagellate-bearing species found only weak effects of reduced pH/increased pCO$_2$[12,13], while other studies found stronger effects[14,15]. A previous field study around a Mediterranean CO_2 seep showed that assemblages shifted from calcifying to agglutinate assemblages, and diversity declined at pH ∼ 7.8[7]. Also, a foraminiferal species living on seagrasses was absent near tropical CO_2 seeps at pH < 7.9 where its calcification was reduced[4].

Here, we investigate changes in the diverse assemblages of tropical sediment-associated foraminifera along natural CO_2 gradients at CO_2 seeps in Milne Bay Province, Papua New Guinea (PNG). Assemblages can be considered acclimatized to high CO_2 through long-term exposure (>70 years of volcanic seep activity) to pCO$_2$ concentrations as predicted for later this century (490 to >1370 µatm pCO$_2$[16]). Previous studies have suggested that CO_2 uptake by photosynthesis elevates pH in the diffusive boundary layer and may thus provide partial

protection against OA to mixotrophic groups[17,18]. The seeps investigated here are located within the 'Coral Triangle', an area of six Central Pacific nations that harbour the most diverse marine ecosystems on earth. The high diversity of the PNG assemblages, consisting of both mixotrophic and heterotrophic taxa (Supplementary Table 1), provided a unique opportunity to investigate the relative vulnerabilities to OA across taxonomic and trophic groupings.

Results

Seawater chemistry contrasted strongly between the 12 control and seep sites, with mean values generally ranging from 8.08 to 7.52 pH units and 369 to 11603 µatm pCO_2, respectively (Supplementary Table 2). One extreme site assumed pH values of ~7.0 and pCO_2 values of >5000 µatm pCO_2. With the exception of that site, calcite and aragonite saturation values at each location remained well above 1.0 (the value at which carbonate theoretically dissolves). Mean total alkalinity was 2326 µmol kg^{-1} (N = 134, SD = 66). Thus 95% of all alkalinity values were between 2197 and 2456 µmol kg^{-1}, a range we used together with the pH measurements from all stations to calculate pCO_2 concentrations (Fig. 1 A). These pH measurements showed a good correlation to the long term averages for the 12 core sites (Supplementary Table 2, R^2 = 0.89, p < 0.0001).

Concentrations of inorganic carbon (IC) in the sediments declined significantly with declining pH (linear model, Fig. 1 B, Table 1), from nearly 100% carbonate sediment (IC = 12%) at ambient pH to nearly zero in most samples below pH 7.7. Sediment organic carbon and nitrogen were unrelated to pH (C: R^2 = 0.01, p = 0.58; N: R^2 < 0.01, p = 0.99). Data found were on a low level typical for coral reef sediments (organic-C: average: 0.28%, SD = 0.21%; N: average = 0.03%, SD = 0.02%). Because of the low level of organic content, the fact that values do not differ between seeps and control areas and that most foraminifera investigated are epibenthic or epiphytic it is unlikely that dissolution driven by interstitial respiratory processes contributed to the observed patterns.

Water collected over the benthos showed no significant (ANOVA, p = 0.1509) difference in the concentration of arsenic between control (mean = 1.62 µg L^{-1}, SD = 0.08 µg L^{-1}) and high (mean = 1.88 µg L^{-1}, SD = 0.50 µg L^{-1}) CO$_2$ sites, and values were in the range on typical marine samples (1–2 µg L^{-1}). Sediments had slightly higher arsenic concentrations directly at the main seeps (which emit almost pure CO_2[5];) compared with the control sites (Seeps: mean = 12.8 mg kg^{-1}, SD = 9.8 mg kg^{-1}, N = 4; Controls: 7.1 mg kg^{-1}, SD = 1.8 mg kg^{-1}, N = 5), most likely reflecting the low carbonate content in the seep sediments. Concentrations in sediments were low compared to those at other volcanic vents (e.g., Ambitle Island, PNG: range: 52–33,200 mg kg^{-1}[19]). In addition, diverse and abundant foraminiferal communities have been described under sediment and water column arsenic concentrations

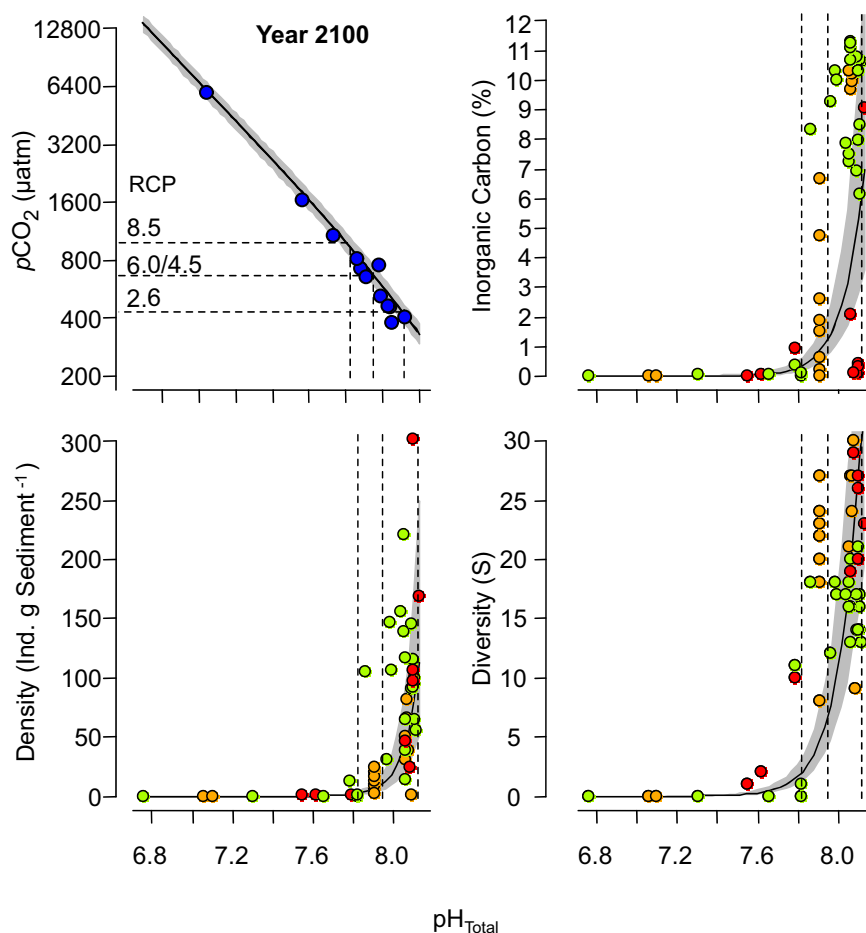**Figure 1 | Changes in sediments and foraminiferal assemblages along pCO_2 gradients at the three CO_2 seep and three control sites.** Relationships between pH$_{Total}$ and pCO_2 in the seawater (A), the total inorganic carbon of the sediment (B), total foraminiferal density (C), and total diversity (D). The black lines represents linear model fits, grey areas mark ranges (A): assuming highest and lowest measured temperatures and alkalinity), or 95% confidence intervals (B–D). Dashed lines demark predicted CO_2 concentrations and corresponding pH values at the end of this century following representative concentration pathways[21] (RCP 2.6: pCO_2 = 421 µatm; SCP 6.0 to 4.5: pCO_2 = 670 µatm; RCP 8.5: pCO_2 = 936 µatm) . Blue symbols in (A) represent pH and pCO$_2$ concentrations at the main stations presented in Supplementary table 2. Other colours represent the sample locations (Upa-Upasina: green, Esa'Ala: orange, Dobu: red).

>10 times those reported here[20]. Arsenic and ten further metal contaminants measured in water above the benthos showed no differences between seep and non-seep sites, and were in ranges expected in pristine seawater (Supplementary Table 3). Temperature loggers recorded only 0.3°C warmer conditions on the benthic surfaces at the seeps compared to the control sites, and annual temperature extremes also only varied by this amount (Seeps: average: 29.6°C, maximum and minimum: 32.2°C and 26.8°C; Controls: 29.3°C, maximum and minimum: 31.8°C and 26.7°C), again in contrast to some other seep sites (e.g., Ambitle surface sediments: seep temperatures: 45–98°C, vs. control site: 30.2°C[19]).

Foraminifera were abundant at control sites (mean densities: 93 individuals g^{-1} sediment, SD = 54 individuals g^{-1} sediment). Densities declined steeply with increasing pCO_2 (Table 1, Fig. 1 C), and foraminifera were almost absent at pCO_2 conditions predicted for the end of this century under all but the most optimistic emission scenarios (RCP2.6, peak at 440 µatm pCO_2,[21]; Fig. 1 A, C). The density of mixotrophic and heterotrophic taxa decreased at the same rate, and their slopes of decline did not differ significantly (Table 1). In other words, both groups followed the same trajectory towards extinction with increasing pCO_2. The slope of decline was less steep for agglutinate compared to calcifying taxa; however, this group was overall rare (1.0% of the assemblage at ambient pH, SD = 1.4%), and they were also absent in any samples at pH < 7.9.

A total of 49 foraminiferal taxa were detected in the 50 sediment samples (Supplementary Table 1). Total foraminiferal diversity also declined with increasing pCO_2 (Table 1, Fig. 1 D).

The comparisons of the slopes for diversity directly mirrored those of densities: there was no significant difference in the rate of diversity loss between mixotrophic and heterotrophic taxa (Table 1). The loss of diversity was significantly slower for agglutinate taxa, but only three taxa were recorded.

Additional dive searches (>5 h total) at Upa-Upasina for living large mixotrophic foraminifera on algal, seagrass and coral rubble substrata revealed that several species can be readily found at the control site (*Amphistegina* spp., *Calcarina* spp., *Heterostegina depressa*, *Marginopora vertebralis*), whereas none could be detected at locations with reduced (<~7.9) pH values.

A permutational multivariate analysis of variance (Permanova) indicated significant differences in foraminiferal assemblage composition between the three sampling locations (Supplementary Table 4). The main difference between locations was that mixotrophic species were dominant at one of the locations (Upa-Upasina) and heterotrophic species dominated at the other two locations (Supplementary Table 5). A distance-based redundancy analysis (dbRDA) showed that the relative contribution of most taxa to the foraminiferal assemblage did not change along the pCO_2 gradient (Supplementary Fig. 1). pCO_2 explained only a small (5.2%) albeit significant proportion of the variation in relative abundances between samples (Pseudo-F = 2.41, p = 0.0133). This confirmed that most taxa disappeared at a similar rate with increasing pCO_2. Exceptions were three species (two *Elphidium* spp. and *Amphistegina lessonii*) which increased slightly in relative importance at intermediate pCO_2 (Supplementary Fig. 1).

Closer inspection of the three samples that had intermediate foraminiferal densities at <7.9–8.0 pH (Fig. 1) showed that most of their foraminifera were *Amphistegina* spp. and *Elphidium* spp., i.e., taxa that appeared to increase in relative importance with elevated pCO_2. However, many of these specimens had a corroded or pitted appearance (Fig. 2). This appearance was not detected in any of the control samples in Milne Bay at present-day pCO_2 conditions, or in sediment core slices >1000 yr of age from the Great Barrier Reef ([22], Fig. 2). The pitted appearance is similar to that observed in another *Amphistegina* species under experimental CO_2 increase[23].

Discussion

Foraminiferal density and diversity at the control sites in PNG were high and similar to those observed on the Great Barrier Reef[22,24] or other sites in PNG[25]. Our data show no sign of acclimation by benthic foraminifera to high pCO_2, although a proportion of genotypes will have lived near the seeps for many generations (their reproduction is partly non-dispersive asexual, as well as through gametes). Our analyses along the pH/pCO_2 gradients around the seeps in PNG suggested that all common tropical foraminiferal species will likely be ecologically extinct at the CO_2 conditions predicted for the year 2100, except under the most optimistic scenario. However, that scenario is unlikely, requiring immediate drastic emission cuts and negative net emission (i.e. carbon sequestration) in the second half of this century[26].

Several mass extinctions of deep sea benthic foraminifera occurred in the geological past, most of which were linked to increased pCO_2 and/or temperature[27,28], but some geological studies from shallow reef environments also observed increased foraminiferal dominance when corals became rare[29]. None of these previous extinctions were as severe as the ecological or even taxonomic extinction in shallow carbonate areas we predict. Previous natural pCO_2 increases occurred one to two orders of magnitude slower and were associated with less reduced calcite or aragonite saturation states than the anthropogenic increases presently observed[28].

Contrary to our initial hypothesis, no shift towards mixotrophic taxa was observed. We assumed that photosymbiont-bearing taxa might be less vulnerable to OA because carbon fixation may increase pH in their diffusive boundary layer[18]; this can lead to pH differences of >0.8 units between day and night[17,18]. A recent study in foraminifera, however, showed that these increases cannot compensate for decreased pH in ambient water[30]. We hypothesized that agglutinate taxa which do not rely on calcification might replace calcifying species. In our study, density and diversity of agglutinate taxa declined less steeply than calcifying taxa. However, agglutinate taxa were too rare to fill the niches vacated by calcifying taxa.

Carbonate sediments at seeps disappeared at calcite or aragonite saturation states >1.0 (Supplementary Table 2). Previous experiments have shown test dissolution and corrosion in temperate heterotrophic foraminifera at >900 µatm pCO_2[31]; although one species

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Table 1 | Results of linear models describing the response of sediment inorganic carbon, foraminiferal density and diversity to decreased pH. Density and diversity data are further split into a) mixotrophic vs. heterotrophic taxa, and b) calcifying vs. agglutinate taxa. A statistical comparison of the slopes for these comparisons is also given. Models were fitted after natural log transformation of the dependent variable

| Source	Slope (SE)	t	P	R^2
Inorganic Carbon	9.60 (0.94)	10.22	<0.0001	0.68
Densities				
Total	13.20 (1.11)	11.86	<0.0001	0.74
Mixotrophic	13.44 (1.18)	11.44	<0.0001	0.73
Heterotrophic	11.14 (1.17)	9.52	<0.0001	0.65
Mixo- vs. Heterotrophic		−1.387	0.169	
Calcifying	13.13 (1.11)	11.86	<0.0001	0.74
Agglutinate	5.50 (1.99)	2.77	0.0081	0.12
Calcifying vs. Agglutinate		−3.35	0.0012	
Diversity				
Total	9.25 (0.86)	10.75	<0.0001	0.70
Mixotrophic	11.22 (1.10)	10.63	<0.0001	0.70
Heterotrophic	10.33 (1.17)	8.83	<0.0001	0.61
Mixo- vs. Heterotrophic		−0.83	0.4100	
Calcifying	11.26 (1.07)	10.49	<0.0001	0.69
Agglutinate	5.79 (2.16)	2.68	0.0100	0.11
Calcifying vs. Agglutinate		−2.27	0.0256	
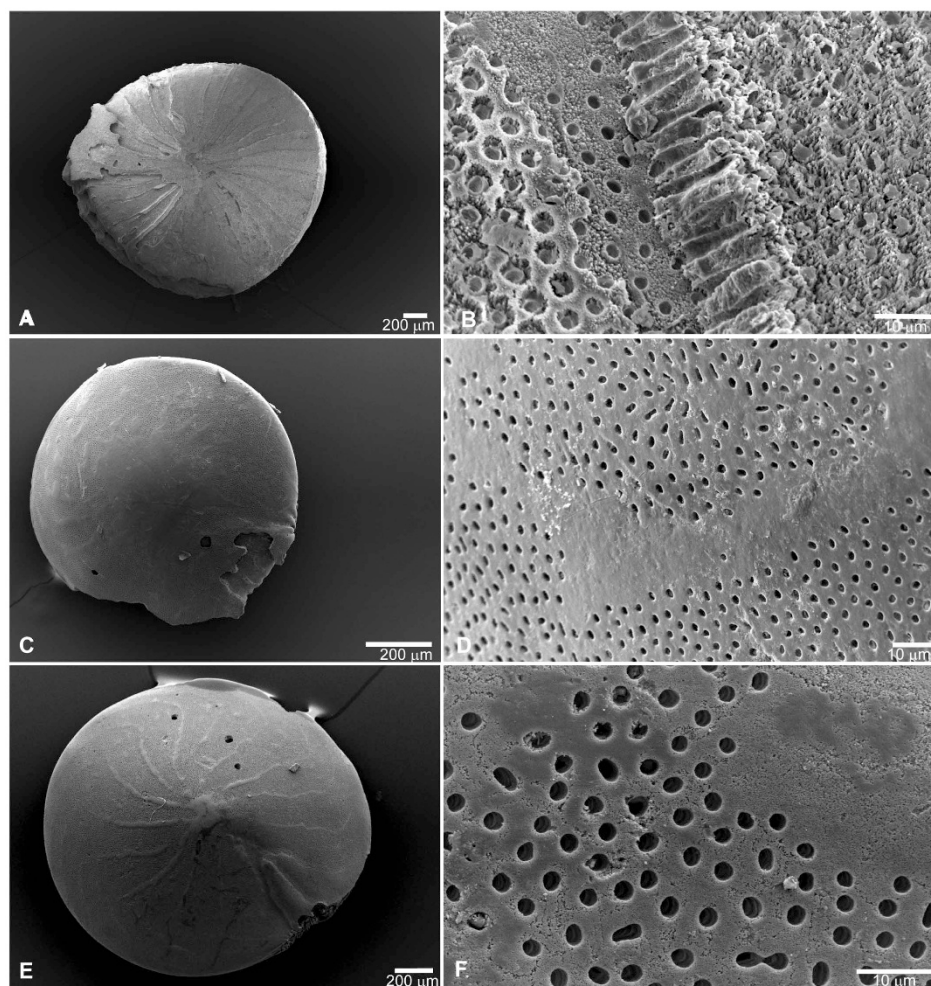
Figure 2 | Scanning Electron Micrographs of *Amphistegina* spp. (A–B) illustrate specimens with corroded and pitted appearance, as found in many foraminifera from sample locations with pH 7.9–8.0. The example shown is from "Esa'Ala elevated pCO_2" (see Table 1), where average pCO_2 over 15 samples was 444 μatm. (C–D) represent a sample from the control location near the Esa'Ala seep (average pCO_2: 369 μatm, Table 1). (E–F) show a sample from a sediment core slice of the Great Barrier Reef (Edward 7, 130–140 cm depth), carbon dated as 1361 years before present (68.5% probability interval: 1157–1564[22],). This sample illustrates that the test corrosion observed near CO_2 vents is not part of the 'normal' taphonomic process.

still calcified at 1900 pCO_2[32]. However, our electron microscopy and sediment inorganic carbon data showed corrosion of foraminifera at 7.9–8.0 pH, and absence of biogenic carbonate accumulation, suggesting that carbonate dissolution began at pCO_2 levels of ~450 μatm. Dissolution of foraminifera and sediment was previously observed under elevated pCO_2 and can start at aragonite saturations states above 3[33,34]. Indeed, most biogenic carbonates dissolved at much higher saturation values than predicted from abiotic carbonates[35]. Thus, in addition to the described direct ecological impacts, the loss of benthic foraminifera, together with dissolution and loss of biogenesis of carbonate by other organisms under near-future pCO_2 conditions may also have far-reaching ecological flow-on effects.

Methods

50 sediment samples were collected during two expeditions to the seep sites[5] in August 2010 and April 2011. Samples were collected at various distances from the three seeps (Esa'Ala, Upa-Upasina, Dobu Island) and their control sites[5]. Samples of the top 1 cm sediment were sourced from 4 to 15 m depth. At each site, three haphazard samples were taken, and pooled into one sample.

For the estimation of foraminiferal abundances, sediments were rinsed over a 63 μm sieve. After drying (>24 h, 60°C), all foraminifera were collected from subsamples until 200 specimens per sample were obtained. This yield could not be achieved for some of the samples collected near the seep sites. In that case, all available sediment was searched. We collected only intact specimens which showed no sign of degradation and little damage ('optimally preserved', sensu[36]) under the dissection

microscope at 25× magnification. These specimens are regarded as a good representation of the present-day (time averaged over the last few years) biocoenosis[36]. Taxa were determined under a dissection microscope, following Uthicke et al. 2010[24]. The dry weights of both sediment and foraminifera were determined to calculate foraminiferal densities. A subsample of foraminifera was observed via Scanning Electron Microscopy (SEM) in order to identify signs of corrosion. Organic matter was removed by incubating the tests in 2% NaClO for 1 h at 60°C. Foraminiferal tests were then dehydrated in 100% ethanol, mounted on SEM stubs and sputter-coated with gold and visualized on a JEOL JSM-5410LV scanning electron microscope.

A subsample of the sediment prior to rinsing and sieving was dried and ground for total carbon and nitrogen determination. Samples were analyzed on a Truspec C/N Analyser (Leco). After acidification (2 M hydrochloric acid), organic carbon in the sediments was measured using a TOC-V Analyser (Shimadzu, equipped with a SSM-5000A Solid Sample Module).

Arsenic concentrations in sediments were determined on acid digested (HNO_3/ $HClO_4$) subsamples, by Hydride Generation Atomic Absorption Spectrometry using a Thermo SOLAAR M Atomic absorption spectrometer. To assess surface sediment temperatures, six temperature loggers (TidbiT v2, Hobo Data loggers) were deployed on the substrata of all seep and control sites for 363 days (April 2011 to April 2012; one logger from Upa-Upasina failed and data are reported for 5 loggers only).

Seawater carbonate chemistry data were based on those presented in[5], complemented by additional samples from April 2011 following the same procedures and based on total alkalinity and dissolved inorganic carbon (DIC) measurements. Arsenic and 10 common heavy metal pollutants were analysed from triplicate (unless marked otherwise in Supplementary Table 3) samples from each of the seep and control sites on an ICP-MS using an octapole reaction system to limit matrix interferences. Samples for these analyses were collected in two opposite seasons, in May and December 2012.

Linear models were used to test for relationships between average pH and the dependent sediment chemistry variables, and foraminiferal total density and diversity, and density and diversity of individual groups. Models were fitted after log transformation (natural logarithm) of the dependent variable. The initial models included depth and pH, but depth was removed from the final models because it did not explain a significant amount of variation for any of the parameters (Supplementary Table 6). Slopes of two groups were compared by adding 'groups', 'pH' and their interaction term into the model and accepting slopes as homogenous when the interaction term was non-significant.

Distance-based redundancy analysis (dbRDA) was used to investigate patterns in assemblage composition across samples. Initial permutation tests showed that depth had no effect of assemblage patterns (Pseudo-F = 1.62, p = 0.0958), but location (Esa'Ala, Upa-Upasina and Dobu Island) affected distributions (Pseudo-F = 6.57, p < 0.0001). These location effects were removed (partialled out) because they were not of interest in the context of our study. The mean pH value for each sample was converted to pCO_2 and used as environmental variable. DbRDA was conducted on a Bray-Curtis distance matrix of fourth-root transformed relative abundance data.

Single-factor permutational multivariate analysis of variance (PERMANOVA) was used to investigate the significance of differences in assemblage composition between sample locations. PERMANOVA post-hoc tests presented here were based on 10,000 permutations, using type III sums of squares and permutation of residuals under a reduced model. Subsequent to PERMANOVA, similarity percentage (SIMPER) was used to investigate which taxa contributed most to between-group differences. DbRDA and linear model analyses were performed in R. PERMANOVA and SIMPER analyses were conducted in Primer 6.0.

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Acknowledgements

Authors contributions

S.U. conducted and designed experiments, analysed data and wrote the MS. P.M. Analysed data and foraminiferal samples, and contributed to the writing. K.F. conceived the overall seep project and contributed to writing and analysis.

Additional information