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Millennium-scale records of benthic foraminiferal communities from the central Great Barrier Reef reveal spatial differences and temporal consistency

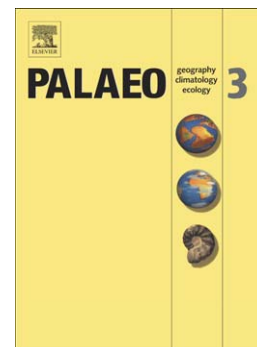Claire E. Reymond, George Roff, Allan R. Chivas, Jian-xin Zhao, John M. Pandolfi

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Millennium-scale records of benthic foraminiferal communities from the central Great Barrier Reef reveal spatial differences and temporal consistency

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Abstract

Understanding long-term community dynamics and the ways in which they respond to major disturbances is a central management theme within coastal marine ecosystems. River outputs from the Queensland coastline directly affect inshore marine communities of the Great Barrier Reef (GBR), Australia. Of these, the Burdekin River exports the highest volume of terrestrial runoff. Following European settlement in the mid-19th century, over three quarters of the native vegetation from the Burdekin catchment was cleared for agricultural purposes. Despite such extensive historical catchment modification, the impact of these changes on the inshore GBR is largely unknown, primarily due to the paucity of long-term ecological data. To assess the effects of modern land-use change on inshore reef environments and to establish an historical baseline of community structure, we examined the sedimentary geochemistry and benthic foraminiferal assemblages of eight sediment cores collected from two coral reefs situated inside (Pandora) and outside (Havannah) an inner-shelf sediment prism formed during the Holocene. Foraminiferal community structure was reconstructed from the past millennium, and the time series was constrained using U-series dating of coral fragments within the cores. Environmental records were reconstructed using stable carbon isotopes ($\delta^{13}C$) and elemental C:N ratios from bulk sediment samples. Non-parametric analysis of community structure in benthic foraminifers indicated no change in community structure through time at either reef. Despite this apparent ecological persistence through time, significant differences in foraminiferal community structure were observed between the two reefs. The communities were clearly characterised by different functional groups; heterotrophic genera were persistent within, and symbiont-bearing genera were persistent outside, the Holocene inshore sediment wedge. We found no difference in the source of

organic matter (interpreted from $\delta^{13}C$ values) either between reefs or through time, yet elemental C:N ratios indicated a difference in the amount of organic matter between reefs. The influence of the Holocene inshore sediment wedge was demonstrated by the dissimilarity in sedimentary C:N ratios between the two reefs.

Keywords: Historical range of variability, community ecology, persistence, benthic foraminifers, Palm Island, Great Barrier Reef, Holocene, coral reef.

1. Introduction

Historical perspectives provide a frame of reference for understanding modern ecological patterns and processes. Palaeoecology contributes invaluable insight regarding ecological trends across timescales prior to modern environmental pressure (e.g. Greenstein and Pandolfi, 2008; Lybolt et al., 2011; Roff et al., 2012). Landscape modifications are impacting coastal marine systems globally (Pringle, 2001), and runoff of pollutants and nutrients into coastal waters significantly impacts upon the quality of coastal habitats (Fabricius et al., 2005; Sandin et al., 2008). The intensity and cumulative impacts of human activities on the ecological condition of marine communities and their spatial distribution are of growing concern (Halpern et al., 2008). Understanding how coastal marine communities functioned prior to landscape modification by humans requires a palaeoecological context, which we use here.

Catchments adjacent to the Great Barrier Reef (GBR), Australia, have undergone large-scale land clearing since European settlement in the mid-19th century (Furnas, 2003). The Burdekin River is the second largest catchment adjacent to the GBR, supplying the highest volume of terrestrially-derived sediment into the inshore central

GBR (Lewis et al., 2007). The GBR hinterland has undergone major catchment modification since European settlement, with up to 80% of the Burdekin catchment cleared for cattle grazing and substantial modification for horticulture and urban development (Haynes and Michalek-Wagner, 2000; Neil et al., 2002; McCulloch et al., 2003a; Lewis et al., 2007). Previous studies show considerable impacts on the ecology of coral reefs due to enhanced terrestrial runoff (van Woesik and Done, 1997; McCulloch et al., 2003a; Fabricius, 2005). Nevertheless, without an understanding of long-term trends in coral reef diversity and function, it is difficult to assess the extent of this anthropogenic footprint.

Weather patterns are known to greatly influence ecosystems and on a global scale have varied notably throughout the past millennium. Such variations in climatic systems call for high-resolution localized proxy records (reviewed in Jones et al., 2009), which are better represented in the Northern Hemisphere compared to the Southern Hemisphere (Jones et al., 2001; Jones and Mann 2004). Yet, what is known from proxy records suggests there was an increase in La Niña activity during 1520-1660 A.D., followed by a reduction in La Niña intensity and an increase in frequency of El Niño between 1600-1780 A.D. (Gergis and Fowler, 2009), which broadly coincides with the Maunder Minimum period of low solar variability 1645-1715 A.D. (Reid, 1997). Additionally, coral Sr/Ca-based SST reconstructions show that the central GBR experienced a cooling period of 0.2 - 0.3°C below the long-term average between 1565-1700 A.D. but experienced an anomalously warm period between 1700-1870 A.D. with similar temperatures to the early 1980s (Hendy et al., 2002). However, the Hendy et al. (2002) record is based on a 5 yr average, and thus can be biased by seasonality change that may affect seasonal difference in coral extension

rates. For instance, if the winter-time growth rate during 1565-1700 A.D. was higher than the whole-period mean, then this can create an artefact of cooling due to the fact the winter-time growth was volumetrically higher than the whole-period mean.

Benthic foraminifers have been successfully used as biological indicators to reconstruct marine conditions and environmental trends (Murray, 1991). This is primarily due to their high taxonomic diversity, prolific abundance, specific ecological requirements, relatively short life cycles (months to years) and because the carbonate tests (exoskeleton) preserve well in the fossil record. The distribution and diversity of modern benthic foraminifers has been studied both for palaeoenvironmental interpretations (Murray, 1991; Sen Gupta, 1999; Murray, 2006) and modern ecological status of disturbed habitats (Narayan and Pandolfi, 2010). Foraminiferal community structure has been used to reconstruct palaeoclimate (Wollenburg et al., 2007), palaeoenvironments (Oldfield et al., 2003), long-term records of eutrophication (Barmawidjaja et al., 1995), modern changes in water quality (Hallock et al., 2003) and sea level (Horton et al., 1999; Edwards and Horton, 2000). Recently, researchers have used the proportion of foraminifers in different functional groups (i.e. opportunistic, heterotrophic and symbiotic) to infer water quality gradients in coral reef and other coastal marine environments (Hallock et al., 2003; Narayan and Pandolfi, 2010; Schueth and Frank, 2008; Uthicke and Nobes, 2008; Uthicke et al., 2010).

Historical water quality can be reconstructed by examining components incorporated into marine sediments (Torgersen et al., 1983; Bird et al., 1995a; Wilson et al., 2005; Lamb et al., 2006; Tsujimoto et al., 2008). Several studies have examined the utility

of stable carbon isotopes (δ^{13}C) along with elementary C:N ratios to reconstruct changes in transported organic matter (Thibodeau et al., 2006; Tsujimoto et al., 2008; Krull et al., 2009). Despite an understanding of the carbon and nitrogen cycle in contemporary coastal zones of the GBR (Alongi and McKinnon, 2005; Fabricius et al., 2005; Cooper et al., 2007), little is known about historical water quality from δ^{13}C and elemental C:N sources. The origin of organic matter in marine sediments, as determined by C:N ratios, is distinguished because of the rich abundance of proteins (Rullkötter, 2006) and the absence of cellulose in marine algae compared to vascular plants (Siegel and Siegel, 1973). The C:N ratio indicates the likely origin of organic matter as either marine (4-10) or terrestrial (>15) (Prahl et al., 1980; Wakeham, 2002). Carbon fixation during photosynthesis discriminates against ^{13}C and depends on the photosynthetic pathway; fractionation in C_4 pathways (-16‰ to -12‰) differs from C_3 pathways (-29‰ to -25‰) and again from marine algae (-22‰ to -20‰) (O'Leary, 1988; Meyers, 1994). Historical evidence from elemental and isotopic records allows retrospective studies of past environmental conditions, and therefore provides a technique to correlate past community structure with long-term water quality trends.

Here we determine the history of benthic foraminiferal communities and terrestrially derived organic matter in reefs adjacent to the Burdekin catchment following European settlement using precisely dated cores extracted from two reefs of the Palm Island region, central GBR (Figure 1). The main objectives of this study are: (1) to identify and reconstruct the source (e.g. marine or terrestrial) of organic matter from the sediment cores, (2) to determine the historical range of variability in foraminiferal community structure over the past millennium, and (3) to assess the long-term

influence of transported organic matter on the taxonomic composition and diversity of benthic foraminiferal communities.

2. Methods

2.1. Study site and background hydrodynamics

Pandora and Havannah reefs are located in the Palm Islands group of the GBR, ~130 km NW from the mouth of the Burdekin River (Figure 1). Pandora reef is situated on the boundary of a Holocene inshore sediment wedge (Larcombe & Woolfe 1999), while Havannah reef is located approximately 10 km seaward (Figure 1). The Burdekin River is the second largest watershed along the GBR and the single largest contributor of freshwater and sediment to the central GBR shelf. Currents and flood plumes from the Burdekin River can travel on average 200 km north and up to 500 km from the river mouth, and are strongly influenced by south-easterly trade winds and Coriolis forces (Lewis et al., 2006). The river discharge from flooding events affects the inshore reef by decreasing salinity (King et al., 2001), re-suspending and delivering sediment (Fabricius and Wolanski, 2000; Bainbridge et al., 2012), and increasing micronutrients (Lewis et al., 2007).

2.2. Field methodology

Sediment coring was conducted at eight localities on the leeward reefs (protected from the prevailing south-easterly swell) of Pandora and Havannah Island (Figure 1, insert). Using SCUBA, four ca. 2-5 m sediment cores (100 mm diameter aluminum pipe, 1.6 mm wall thickness) were recovered from the reef slope (5m depth) at each site ($n = 8$). The unconsolidated reef matrices, consisting of coral and molluscan

components within a muddy to coarse-grained sand, were extracted using a modified percussion technique (Dardeau et al., 2000). This required several divers, on rotation, to manually operate a slide hammer to force the core through the reef matrix, cap the core and lift it out of the reef. Core recovery of reef matrix was measured by determining penetration depth of the core barrel in the reef and the sediment compaction after extraction. Upon return to the laboratory, cores were longitudinally sectioned into two halves using a circular saw. One half was segmented at 5 cm increments to determine core chronology, and foraminiferal and sediment composition, and the other half archived in a -1°C freezer. As the accretion rate (as calculated from the core chronology) and length of cores differed, 5 cm sub-samples were selected at 50 yr intervals (as defined by U-series chronology detailed below) to allow temporal replication among cores. Foraminiferal community structure was determined by sieving the sediment from each 5 cm sub-sample through a 125 μm sieve and identifying the first 200 individuals encountered to genus level using descriptions based on Loeblich and Tappan (1994). In 8 out of 112 cases, less than 200 individuals were collected due to the small sediment content in the 5 cm sub-sample.

2.3. *Thermal Ionization Mass Spectrometry Uranium-Series Dating*

Chronologies of each core were established through high-precision uranium-series dating of the coral rubble within the core sections. To establish a reliable chronological framework for the cores, 47 representative samples of mainly fast-growing branching coral fragments (n = 5-8 per core) were dated using Thermal Ionization Mass Spectrometry (TIMS) outlined in Zhao et al. (2001, 2009) and Clark et al. (2012) in the Radiogenic Isotope Facility at the Centre for Microscopy and

Microanalysis (CMM) of the University of Queensland. Where live coral was present on the top layer of the core it was treated as 2008 A.D. (referring to the year when the cores were collected); however, if dead coral was present on the surface an additional U-series age was obtained to constrain the age/depth relationship. Great care is needed for dating samples less than a few hundred years of age by TIMS (see Zhao et al., 2009, for review), with particular attention paid to procedural blank corrections as well as corrections for the contribution of initial/detrital ^{230}Th which is proportionally much higher than in older samples. Detailed correction procedures are outlined in Zhao et al. (2009), Clark et al. (2012) and Roff et al., (2012). For the initial/detrital ^{230}Th correction, we adopt a two-component mixing model to calculate the initial ^{230}Th/^{232}Th value for each specific sample (see Table S1), rather than applying a commonly used generalized global ^{230}Th/^{232}Th initial mean.

2.4. Geochemical analysis

Carbon and nitrogen elemental abundances and carbon-isotope composition were analyzed on a Carlo Erba NCS1500 elemental analyzer (EA) coupled to a Micromass Prism III mass spectrometer (University of Wollongong). To determine total organic carbon (C_{org}) and total nitrogen (N) content, ~10 g bulk sediment samples were freeze-dried, powdered and reacted twice with 10% HCl to remove all calcium carbonate, and washed with deionised water to remove excess HCl. The remaining material was dried for 48 h at 60°C before loading in 5 x 9 mm tin capsules. Samples were loaded into a 93-well carousel holder. Each analytical run started with eight elemental standards. During the run two elemental standards were analyzed subsequent to every 10 samples. The overall reproducibility of δ^{13}C determinations with this method, including typical sample inhomogeneities and combustion

variability is 0.3 ‰. The elemental calibration was carried out with ANU (Australian National University) sucrose (42.11% C; -10.47‰ δ^{13}C), urea (19.98% C; 46.89% N; -36.46‰ δ^{13}C), atropine (70.56% C; 4.84% N; -28.53‰ δ^{13}C), benzoic acid (-28.34‰ δ^{13}C), IAEA-C7 Standard Reference Material (SRM) Oxalic Acid (-14.48‰ δ^{13}C), IAEA-C8 (SRM), Oxalic Acid (-18.3‰ δ^{13}C), and NIST (National Institute of Standards and Technology, SRM) 1547 (45.3% C; 2.88% N; -25.88‰ δ^{13}C).

2.5. Data Analysis

2.5.1. Multivariate analyses

We reconstructed benthic foraminifer assemblages using the relative abundance and diversity of genera. Multivariate analyses were conducted to test the effects of sample age and reef site on community structure with the geochemical covariates C:N and δ^{13}C using PRIMER 6.1.10 (Primer-E Ltd, UK) with the PERMANOVA add-on (Anderson et al., 2008). Prior to calculation of a Bray-Curtis similarity matrix, the raw abundance data were square root transformed and normalized to reduce the influence of genera with high abundance; this transformation increases the weight of rare species in the sample comparisons (Somerfield and Clarke, 1995). Community similarity among all samples was calculated using the Bray-Curtis similarity index (Bray and Curtis, 1957). As the design was unbalanced due to unequal temporal replication, all statistical analyses were calculated using the permutation method in PERMANOVA (a routine for testing the response of one or more variables to a number of factors in an analysis of variance {ANOVA} design), as described in Anderson (2001) and McArdle and Anderson (2001). The assumption of homogeneity of variance was confirmed for both factors using PERMDISP, a distance-based test

for homogeneity of multivariate dispersions. Where there was an interaction between one of the factors in the model and a covariate, a linear distance model was run to assess the variance of the predictor variable using the DISTLM function in PERMANOVA. A 2-dimensional non-metric multidimensional scaling (nMDS) ordination was used as a visual representation of the compositional differences among assemblages.

2.5.2. Univariate analyses

For each core subsample, the Shannon diversity (H'), Pielou evenness (J') and Margalef richness (d') indices were calculated in PRIMER v6 (Clarke and Warwick, 2001). Margalef's index is dependent on sample size and uses species richness; however, the Shannon index assumes individuals are randomly sampled from a community with infinite abundance and therefore applies proportional abundances in the equation. The effects of age and reef upon benthic foraminiferal diversity indices were analyzed using permutation ANOVA. The univariate analysis used the same mixed model structure as the multivariate PERMANOVA, but the resemblance matrix was based on the measurement of Euclidean distance. A full factorial sequential Type I sum of squares model was conducted to test for the effect of the geochemical covariants on each diversity measurement. Where there were no significant effects ($P > 0.05$) and homogeneity of the covariates was confirmed, the covariant was removed and a partial Type III sum of squares mixed model was used. Lastly, spatial and temporal variation in the C:N ratio and $\delta^{13}C$ were tested in PRIMER v6 (Clarke and Warwick, 2001) using the Euclidean distance measurement for the resemblance matrix with a univariate ANOVA following the above methods. Where a significant

effect was detected, an additional pairwise analysis was conducted to examine the spatial or temporal difference in diversity in greater detail.

2.5.3. Geochemical association with foraminiferal community composition

A Mantel test (Mantel, 1967) was used to investigate the relationship between the resemblance matrix of C:N or δ^{13}C and taxonomic similarity in PRIMER using the subroutine RELATE (Somerfield et al., 2002). The sample statistic (*Rho*) was calculated using the Spearman rank correlation between the observed Euclidean distance matrix (either C:N or δ^{13}C) and the Bray-Curtis similarity matrix. The correlation between the matrices (C:N or δ^{13}C and Bray-Curtis similarity) were permutated 999 times using a randomisation technique, which reorders the values of one matrix with the corresponding values in the second matrix to generate an expected distribution that is compared with *Rho* (Sokal and Rohlf, 1995). If the observed measure of *Rho* is sufficiently different from the randomised distribution, then an association between the two matrices is accepted.

3. Results

3.1. TIMS U-series ages

In this study 11 coral genera were used for TIMS U-series dating, the fragments were chosen based on preservation (Table S1). From the TIMS U-series data, the accretion rate was calculated separately for each core. The linear regressions of stratigraphic position (depth) versus age of each core had an $r^2 > 88\%$, implying continuous accretion throughout and a well constrained age-depth correlation. There were only two occurrences of age/depth reversals: one in sample H112BF at 200 cm core depth

(~1681 A.D.) and one in sample H27AZ at 45 cm core depth (~1927 A.D.) (Figure S1; Table S1). The cores recovered from Havannah extend from the modern to ~1050 A.D., and those from Pandora, from the modern to ~1200 A.D. Each 5 cm section equates to 4 - 14 yr of reef matrix growth, with the average section duration being 11 ± 3.5 yr (1-sigma). Additionally, the reef accretion at Pandora and Havannah were comparatively similar throughout the length of the cores (Roff 2010). For the presentation of all figures and tables, the youngest surface sample was rounded up to 2010; we found this appropriate, as the difference to round was less than the standard error for each section.

3.2. Community structure

The non-metric multidimensional scaling (nMDS) ordination shows a clear separation in community composition between Pandora and Havannah reefs (Figure 2A) with no temporal groupings (Figure 2B). Proportional abundances of the foraminiferal community from each reef did not change significantly through time, yet the communities from the two reefs are significantly different from one another. There are high abundances of heterotrophic individuals from Pandora, whereas communities from Havannah are composed mainly of photosymbiont-bearing individuals (Figure 3). *Quinqueloculina, Eponides* and *Spiroloculina* were the most prevalent heterotrophic genera throughout the cores. *Elphidium* was the most abundant opportunistic genus with several common agglutinated opportunistic genera such as *Sahulia, Textularia* and *Clavulina. Calcarina*, *Amphistegina* and *Peneroplis* were the most abundant photosymbiont bearing genera (Table S2). The proportions of functional groups (heterotrophic, opportunistic and photosymbiont-bearing) were constant through time at each site and significantly differed between reef sites (Figure 3). Results from the comparative analysis of Bray-Curtis similarity among

foraminiferal communities, indicates no crossed interaction of reef site and the amount of time separating the communities, no temporal difference among communities from the same reef (Figure 4), and a significant difference in overall similarity between the reefs ($F_{(1,111)} = 29.256$; $p = 0.001$; Table 1).

3.3. Diversity

In total 60 genera were identified with a range of 14-38 genera from each sample. Shannon H' diversity ranged from 2.0-2.5 for all samples, Pielou J' evenness ranged between 0.6-0.8 and Margalef d' richness ranged from 3.0-5.0 (Figure 5). Overall, there were no significant differences in Shannon diversity with respect to reef or age, but a significant difference in Pielou evenness occurred between the two reefs (pseudo $F_{(1,111)} = 4.947$; $p = 0.025$) and a crossed effect of age and reef occurred for Margalef richness (pseudo $F_{(16,111)} = 2.351$; $p = 0.014$; Table 2). Margalef richness differed temporally in < 20% of the samples, twice consecutively at 1210 and 1260 A.D. and again in 1460 A.D (Table S3).

3.4. Geochemical analysis

The C:N ratio was consistently lower from the Havannah cores, which were less variable than those from Pandora reef (Figure 5; Table S4). The average value of C:N from the Havannah cores is within the range of marine-derived organic matter (~10); however, the higher values of C:N from the Pandora cores is typical of terrestrially-derived organic matter (>15). The $\delta^{13}C$ values from all cores were within a range of -15 to -10‰, with an average of -12‰ (Figure 5; Table S4). No significant difference in $\delta^{13}C$ values occurred through time or between reefs but a significant interaction

occurred between age and reef for C:N ratios (pseudo $F_{(16,111)}$ = 2.20, p = 0.016; Table 3). Pairwise comparisons showed significantly higher C:N ratios in the sediment from Pandora reef (Table S5). There was no association observed between the $\delta^{13}C$ Euclidean distance and the difference in community similarity (Rho = 0.06; p = 0.11), although communities with greater separation in C:N ratios were less similar in composition (Rho = 0.30; p = 0.001).

4. Discussion

We present a 1000 yr record of benthic foraminiferal community composition to determine the natural range of variability prior to land use changes following European settlement (mid-19th century). No significant differences in foraminiferal community composition were detected within sites throughout the study period, despite Ba/Ca records indicating peak sediment fluxes during 1968, 1974 and 1981 A.D. (McCulloch et al., 2003a), vegetation clearance and high volumes of cattle throughout the early 1900s (McCulloch et al., 2003b), and climatic variability, such as extreme and protracted ENSO events in the 20th century (Gergis and Fowler, 2009). However, significant spatial differences existed between foraminiferal communities at Havannah and Pandora reefs, and these differences are closely associated with the C:N ratios within the reef sediment.

4.1. Spatial and temporal patterns in foraminiferal communities

Benthic foraminifers inhabit a number of tropical marine ecosystems (Table S2) and assemblages have the capacity to transform rapidly under changing environmental conditions (Jorissen, 1987; Sen Gupta and Aharon, 1994; Culver and Buzas, 2000;

Alve, 2003; Darling et al., 2009). Additionally, the functional traits of foraminifers can be used to characterize organic flux and oxygen availability (van der Zwaan and Jorissen, 1991; Jorissen et al., 1992), salinity (Hottinger, 1983; Hallock and Glenn, 1986), eutrophication gradients within coastal marine waters (Alve, 1995; Culver and Buzas, 1995; Gooday et al., 2009; Narayan and Pandolfi, 2010) and water quality in shallow coral reef environments (Hallock et al., 2003; Schueth and Frank, 2008; Uthicke and Nobes, 2008). We found a predominance of photosymbiont-bearing genera at Havannah reef, and a predominance of heterotrophic genera at Pandora reef (Figure 3). Differences in the relative abundance of functional traits between the two sites indicate variability in sedimentation, organic matter and light conditions, as observed in modern studies (for example, Hallock et al., 2003; Schueth and Frank, 2008; Uthicke and Nobes, 2008). The heterotrophic assemblages from Pandora reef indicate organic matter enrichment associated with terrestrial runoff (C:N > 15). The photosymbiont-bearing foraminiferal assemblages from Havannah reef indicate reduced terrestrially derived organic matter (C:N < 10), which could be due to either a lower influence of river runoff or a greater level of mixing with oligotrophic water. Moreover, the foraminiferal communities could also be responding to their position inside or outside the Holocene sediment wedge (Figure 1; Larcombe & Woolfe 1999). Pandora reef sits inside the wedge and experiences higher rates of sediment re-suspension, turbidity and terrestrial influence than Havannah reef, which lies ~10 km outside the wedge.

At the generic level, foraminiferal communities from Pandora reef changed slightly after the mid-19th century (Figure 3B): *Amphistegina* abundance decreased, while *Ammonia* and *Calcarina* increased. Although *Amphistegina* and *Calcarina* are

widespread photosymbiont bearing reef-flat genera throughout the Indo-Pacific region (Sen Gupta 1999), *Calcarina* commonly shows greater flexibility in habitat preference than predicted by its functional grouping (e.g. Renema and Troelstra 2001). Similarly, *Ammonia* is a known estuarine or brackish water genus (Murray 1991) and its increase in abundance might indicate a shift in freshwater. These minor increases in *Calcarina* and *Ammonia* abundances from Pandora reef might be connected to the abrupt freshening and cooling of the southwestern Pacific at the end of the Little Ice Age in the late 19th century (Hendy et al. 2002). Additionally, since the 15th century, foraminiferal communities from Havannah reef are observed to decrease in heterotrophic genera and slightly increase in opportunistic and photosymbiont bearing genera but showed no abrupt change in the late 19th century.

Analysis of the diversity of modern benthic foraminifers is not clearly predicted by environmental conditions. For example, highly diverse foraminiferal communities have been found to occupy both fluvial influenced embayments (Narayan and Pandolfi, 2010) and oligotrophic reef environments (Langer and Lipps, 2003). In our study, we observed no differences in Shannon diversity (H'), but significantly greater Pielou evenness (J') at Havannah than Pandora reef and a mixed spatial and temporal response of Margalef richness (d'). The indices show more variability from Pandora than Havannah reef and may imply some differences in environmental stability between the two sites. Thus, benthic foraminiferal diversity alone is a poor indicator of environmental conditions at our two study sites. Only evenness varies between the reef sites. Among other studies of coral reef organisms, long-term patterns in species diversity have also been observed to persist in the presence of significant environmental fluctuations (Pandolfi, 1996; Tager et al., 2010; Reymond et al., 2011).

Overall, the natural range of foraminiferal community composition shows some minor variation but principally temporal consistency as evident from the high community similarity through time regardless of the length of time separating the communities (Figure 4). This implies that heterotrophic foraminiferal communities within the Holocene inshore sediment wedge were able to withstand 5-10 fold sedimentation increases since large-scale catchment modification. Similarly, the temporal consistency in the species composition and diversity of symbiont-bearing foraminiferal communities from Havannah suggests recent fluvial runoff has not altered the water quality outside the Halifax Holocene inshore sediment wedge sufficiently to affect the ecological structure of foraminiferal communities.

4.2. Evidence from elemental and isotopic markers

Elemental C:N and isotopic $\delta^{13}C$ were used to distinguish the origin of organic matter within the ancient sedimentary deposits (Wilson et al., 2005). The C:N ratio from sediment can be used to differentiate the marine vs. terrestrial origin of organic matter (Prahl et al., 1980; Wakeham, 2002). The C:N ratio for marine algae ranges between 4-10 (Meyers, 1994), while for terrestrial organic matter the C:N ratio is generally above 15 (Prahl et al., 1980; Wakeham, 2002). Sediment samples from the Havannah cores have a C:N ratio comparable with that of marine algae, likely reflecting phytoplankton blooms with terrestrial and oceanic mixing that occurs during flooding events (Devlin et al., 2001; Devlin and Brodie, 2005). Even though there is a decreasing trend in C:N ratio progressively from the younger sediment of the Pandora cores, the C:N ratio still remains on average >15, implying a strong influence from terrestrially derived C_4 vascular plants. When comparing the two reef communities, assemblages appear to be structured according to the C:N ratio. Pandora reef on

average has a higher C:N ratio and greater abundance of heterotrophic foraminifers, in contrast to Havannah reef which has a lower C:N ratio and a higher abundance of photosymbiont-bearing foraminifers, indicating clear oligotrophic waters Thus, benthic foraminifer composition and abundance in coastal marine habitats of the GBR are closely associated with hydrodynamic flux in organic matter.

The fraction of terrestrial organic carbon in marine sediment commonly varies with the distance from a river mouth and the source of organic material (Sackett and Thompson, 1963; Shultz and Calder, 1976; Schwartz et al., 1986; Bird et al., 1992 and 1994). Similarly, from the geochemical marker, pentacyclic triterpenoid alcohol (PTA), trace organic compounds from terrestrial plants reach the inner GBR after flood events, with the bulk of terrestrial organic matter restricted to the inshore sediment (Currie and Johns, 1989). The mean $\delta^{13}C$ value of local marine organic carbon on the GBR is about -19 ‰ (Torgersen et al., 1983). To the north of our study site, the bays adjoining Hinchinbrook Island (Figure 1) display modern sediment with $\delta^{13}C$ values between -20 and -24 ‰ (Torgersen and Chivas, 1985) and are strongly determined by C_3 mangrove vegetation and sedimentation. These modern studies indicate lower $\delta^{13}C$ values than the historic ranges in sediments from Havannah and Pandora reefs (-15 to -10 ‰). Minor variation in the range of $\delta^{13}C$ could be attributed to energy-related sorting, deposition, oxidation and mixing between autochthonous and allochthonous sources (Smith et al., 2008), or water deficit during plant growth (Merchant et al., 2010). However, the major discrepancy between the values we observed is most likely due to the source of primary productivity and organic burial.

The δ^{13}C values of organic sediment from Pandora and Havannah reefs are best explained by their location in the path of the modern sediment plume that emanates from the Burdekin River. The δ^{13}C values measured from Havannah and Pandora reef indicate the continuous influence of organic terrestrial sources from a dominant C_4 metabolic pathway, which have a typical δ^{13}C value of -12 ‰. This is indicative of native grasses and introduced sugar cane, which is currently the main crop along the Queensland coast since land clearing post European settlement. It also suggests the predominance of native grasses before cropping. Because both vegetation types have the same metabolic pathway we cannot differentiate the changes in land use from this marker alone. Even though our study found no change in δ^{13}C, Bird et al. (1995b) found a 2 ‰ increase in the δ^{13}C values of alkanes extracted from marine sediment in the GBR following land clearing for sugar cane and pasture in the late 1880s along the Johnstone River (about 150 km north of this study site). Despite apparent historical increases in sediment flux (McCulloch et al., 2003), our geochemical analysis from bulk sediments indicate that the composition of transported organic matter has remained constant throughout the last millennium. The long-term history of terrestrial runoff entering the inshore marine waters has shaped the foraminiferal communities at Pandora and Havannah reef before recent catchment modification as evident from the high community similarity through time regardless of the length of time separating the communities.

5. Conclusions

Our analysis of benthic foraminiferal assemblages and their temporal distribution in Pandora and Havannah reefs indicates:

(1) Site variability was greater than temporal variability among foraminiferal communities over the past 1000 yr. There are no significant signs of

community shifts since European settlement or during past climatic fluctuations. Community similarity through time remained constant regardless of the length of time separating the communities.

(2) Diversity was relatively high at both reef sites regardless of the functional groups represented or geochemical signature; however, community evenness was greater with a reduction in terrestrial influence, as evident from the C:N ratios.

(3) Community structure was correlated with spatial changes in the C:N ratios from the core sediment. The relative abundance of the functional assemblages was influenced by the amount of sedimentary organic matter; where a greater abundance of heterotrophic foraminifers were present there was a higher influence of terrestrial runoff, causing lower light conditions and higher amounts of organic matter. A high abundance of photosymbiont-bearing foraminifers occurred in water with a lower influence of organic matter from terrestrial runoff. At our study sites, the threshold between photosymbiont-bearing and heterotrophic foraminifers communities occurred between C:N of 10-15.

(4) Overall, the natural range of foraminiferal diversity and taxonomic composition showed temporal consistency, which implies these communities were able to withstand 5-10 fold sedimentation increases since large-scale catchment modification.

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Figure 1. Regional setting of Havannah and Pandora reefs, Palm Islands group, central Great Barrier Reef (GBR), Queensland, Australia. The main river influence is the Burdekin River with the point of discharge indicated by an arrow (south) and to a lesser degree the Herbert River (north). The direction of these plumes is indicated by arrows. The dashed line is the estimated extent of the Holocene inshore sediment wedge in Halifax Bay (Larcombe and Woolfe 1999). The inset maps show the location of the sediment cores collected from Pandora (P2A, P2B, P3A and P3B) and Havannah (H1A, H1B, H2A and H2B) reefs. (H) - Hinchinbrook Island.

Figure 2. Two-dimensional non-metric multidimensional scaling (nMDS) ordination of benthic foraminiferal assemblages derived from sediment cores taken from Havannah and Pandora reefs, inshore GBR. The nMDS ordination is depicted in two ways; samples grouped by A) reef, and B) 200 yr time intervals.

Figure 3. Core profiles of the relative abundance of benthic foraminiferal assemblages from Havannah and Pandora reefs, GBR. Shown are relative pooled abundance (sum is to 100%) of heterotrophic, opportunistic and symbiont-bearing genera from A) Havannah reef and B) Pandora reef. All heterotrophic genera contributing less than 5% to the overall community were designated as 'other'. Columns illustrate the relative proportional abundance of the genera contributing to each of the functional groups, with the vertical axis expressed as ^{230}Th age in calendar years (A.D.).

Figure 4. Average Bray-Curtis (BC) similarity between communities plotted against the length of time separating the communities ($\pm$ SE) from A) Havannah reef, and B) Pandora reef.

Figure 5. Core profiles of three biodiversity indices, Shannon diversity (H'), Pielou evenness (J'), and Margalef richness (d'), and two geochemical markers, C:N and $\delta^{13}C$ ($\pm$ SE). The vertical axis is expressed as ^{230}Th age in calendar years (A.D.). Shaded area highlights post-European settlement (PES).

Table 1. A two-factor (age and reef) PERMANOVA model with partial (Type III) sums of squares comparing the Bray-Curtis similarity in taxonomic composition of foraminiferal communities from Havannah and Pandora reef. Significance is indicated in bold when $p < 0.05$.

Variable	Effect	df	SS	MS	Pseudo-F	p
Bray-Curtis	Age	21	13342	635	1.147	0.207
similarity	Reef	1	16205	16205	29.256	0.001
	Age x Reef	16	8929	558	1.068	0.312

Table 2. Univariate analysis based on the Euclidean distance of Shannon's diversity (H'), Pielou evenness (J') and Margalef richness (d') using a PERMANOVA two-factor (age and reef) model with partial (Type III) sums of squares for Pandora and Havannah Reefs. Significance is indicated in bold when $p < 0.05$.

Variable	Effect	df	SS	MS	Pseudo-F	p
Diversity (H')	Age	21	1.935	0.092	1.127	0.338
	Reef	1	0.226	0.226	2.758	0.091
	Age x Reef	16	1.065	0.067	0.814	0.685
Evenness (J')	Age	21	0.072	0.003	0.570	0.925
	Reef	1	0.030	0.030	4.947	**0.025**
	Age x Reef	16	0.055	0.003	0.567	0.892
Richness (d')	Age	21	28.205	1.343	3.611	**0.001**
	Reef	1	0.515	0.515	1.386	0.215
	Age x Reef	16	13.996	0.875	2.351	**0.014**

Table 3 Univariate analysis based on Euclidean distance of the δ^{13}C and C:N ratio using a PERMANOVA two-factor (age and reef) model with partial (Type III) sums of squares for Pandora and Havannah Reefs. Significance is indicated in bold when p < 0.05.

Variable	Effect	df	SS	MS	Pseudo-F	p
δ^{13}C	Age	21	78.92	3.76	1.38	0.196
	Reef	1	0.23	0.23	0.08	0.78
	Age x Reef	16	30.07	1.88	0.69	0.77
C:N	Age	21	309.69	14.75	2.85	0.001
	Reef	1	1040.1	1040.1	200.78	0.001
	Age x Reef	16	182.39	11.40	2.20	0.016

Supplementary material.

Figure S1. Plot showing the TIMS U-series age versus depth from each of the 8 cores

collected from Havannah and Pandora Reef, Palm Islands, Australia.

Table S1-S5.

Table S1. Chronologies of each core were established through high-precision TIMS U-series dating of the coral rubble within the core sections.

A two-component initial/detrital ^{230}Th correction was used to calculate the initial ^{230}Th/^{232}Th value for each specific sample (Roff 2010).

Site	Transect ID	Core ID	Sample Depth (cm)	Corrected Depth (cm)	Sample Name	Genus	U (ppm)	±2σ	^{232}Th (ppb)	±2σ	(^{230}Th/ ^{232}Th)	±2σ	(^{230}Th/ ^{238}U)	±2σ	Initial (^{234}U/ ^{238}U)	±2σ	corr. Initial (^{234}U/ ^{238}U)	±2σ	uncorr. ^{230}Th Age (yr.)	±2σ	corr. ^{230}Th Age (A.D.)	±2σ
Pandora	2	A	280	397	P242AG	*Goniopora*	2.6707	0.0023	20.75	0.16	1.528	0.025	0.003919	0.000039	1.1474	0.0013	1.1478	0.0013	373.6	3.7	1798.0	33.0
Pandora	2	A	210	297	P2142AU	*Acropora*	2.7974	0.0026	6.235	0.051	3.265	0.070	0.002403	0.000036	1.1456	0.0014	1.1458	0.0014	229.3	3.4	1829.0	10.0
Pandora	2	A	175	248	P2142BB	*Merulina*	2.5496	0.0023	0.299	0.001	30.25	0.45	0.001170	0.000016	1.1462	0.0012	1.1463	0.0012	111.5	1.5	1901.6	1.7
Pandora	2	A	110	156	P2142BO	*Stylophora*	2.8142	0.0018	5.696	0.042	1.577	0.054	0.001054	0.000030	1.1465	0.0012	1.1466	0.0012	100.4	2.9	1953.4	9.3
Pandora	2	A	50	71	P2142CA	*Goniopora*	2.5482	0.0030	0.779	0.002	25.81	0.29	0.002598	0.000027	1.1469	0.0014	1.1470	0.0014	248.0	3.0	1771.2	3.1
Pandora	2	B	205	428	P2?AB	*Goniopora*	3.0085	0.0038	1.471	0.015	22.11	0.47	0.003561	0.000046	1.1471	0.0016	1.1473	0.0016	339.0	4.0	1681.4	5.1
Pandora	2	B	155	323	P2?AL	*Goniopora*	2.7744	0.0018	29.24	0.20	1.276	0.020	0.004441	0.000045	1.1474	0.0012	1.1478	0.0012	423.5	4.4	1805.0	44.0
Pandora	2	B	145	302	P2?AN	*Pavona*	3.1061	0.0030	7.564	0.054	3.148	0.077	0.002531	0.000047	1.1478	0.0013	1.1479	0.0013	241.1	4.5	1821.0	11.0
Pandora	2	B	55	115	P2?BF	*Goniopora*	2.9096	0.0024	23.216	0.058	0.94	0.02	0.002484	0.000048	1.1470	0.0012	1.1473	0.0012	236.7	4.6	1939.0	34.0
Pandora	2	B	10	21	P2?BP	*Porites*	3.4875	0.0023	23.050	0.092	0.801	0.012	0.001748	0.000022	1.1478	0.0015	1.1480	0.0015	166.4	2.1	1981.0	28.0
Pandora	3	A	290	426	P335AA	*Stylophora*	2.9311	0.0233	1.1061	0.0064	62.78	0.64	0.007800	0.000098	1.1335	0.0084	1.1338	0.0084	754.0	11.0	1265.0	11.0
Pandora	3	A	205	301	P335AR	*Turbinaria*	4.6480	0.0088	10.227	0.061	7.07	0.10	0.005124	0.000052	1.1453	0.0016	1.1456	0.0016	489.5	5.0	1566.0	11.0
Pandora	3	A	135	198	P335BB	*Goniopora*	2.2215	0.0022	3.618	0.018	6.76	0.11	0.003623	0.000045	1.1481	0.0013	1.1483	0.0013	345.1	4.4	1701.2	8.5
Pandora	3	A	80	118	P335BQ	*Goniopora*	3.1138	0.0039	9.045	0.033	3.262	0.066	0.003119	0.000057	1.1470	0.0016	1.1472	0.0016	297.3	5.5	1774.0	14.0
Pandora	3	A	15	22	P335CC	*Goniopora*	2.6898	0.0027	15.103	0.098	0.739	0.046	0.001367	0.000079	1.1462	0.0016	1.1464	0.0016	130.3	7.6	1997.0	25.0
Pandora	3	B	325	407	P3134AC	*Palaustrea*	2.5400	0.0027	0.743	0.004	70.51	0.79	0.006790	0.000051	1.1452	0.0015	1.1455	0.0015	649.0	5.0	1369.3	5.3
Pandora	3	B	260	326	P3134AP	*Acropora*	2.6833	0.0021	7.780	0.083	5.19	0.12	0.004950	0.000067	1.1467	0.0015	1.1470	0.0015	472.0	6.0	1599.0	14.0
Pandora	3	B	215	270	P3134AY	*Acropora*	3.7187	0.0046	3.077	0.028	13.04	0.20	0.003552	0.000027	1.1489	0.0016	1.1490	0.0016	338.1	2.6	1690.3	4.6
Pandora	3	B	170	213	P3134BH	*Pavona*	3.5859	0.0040	0.6638	0.0020	44.99	0.48	0.002742	0.000025	1.1479	0.0016	1.1480	0.0016	261.2	2.4	1754.2	2.7
Pandora	3	B	115	144	P3134BS	*Goniopora*	2.6423	0.0024	9.637	0.063	1.70	0.04	0.002046	0.000035	1.1498	0.0011	1.1500	0.0011	194.5	3.4	1893.0	16.0
Pandora	3	B	60	75	P3134CD	*Goniopora*	3.1643	0.0033	27.98	0.17	0.926	0.015	0.002705	0.000033	1.1471	0.0013	1.1474	0.0013	257.8	3.1	1936.0	37.0

Site	Transect ID	Core ID	Sample Depth (cm)	Corrected Depth (cm)	Sample Name	Genus	U (ppm)	±2σ	^{232}Th (ppb)	±2σ	(^{230}Th/^{232}Th)	±2σ	(^{230}Th/^{238}U)	±2σ	Initial (^{234}U/^{238}U)	±2σ	corr. Initial (^{234}U/^{238}U)	±2σ	uncorr. ^{230}Th Age (yr.)	±2σ	corr. ^{230}Th Age (A.D.)	±2σ
Havannah	1	A	230	305	H112AY	*Goniopora*	3.0429	0.0038	7.151	0.045	8.20	0.10	0.006364	0.000050	1.1617	0.0014	1.1620	0.0014	599.8	4.8	1460.0	11.0
Havannah	1	A	200	266	H112BF	*Alveopora*	2.8955	0.0027	7.434	0.027	4.759	0.079	0.004035	0.000057	1.1493	0.0013	1.1495	0.0013	384.0	5.5	1681.0	12.0
Havannah	1	A	145	192	H112BQ	*Alveopora*	3.2542	0.0027	11.427	0.071	4.402	0.090	0.005104	0.000078	1.1480	0.0012	1.1483	0.0012	486.6	7.5	1597.0	17.0
Havannah	1	A	105	139	H112BY(V)	*Goniopora*	2.5310	0.0020	22.89	0.10	1.484	0.015	0.004431	0.000032	1.1454	0.0013	1.1458	0.0013	423.2	3.1	1775.0	38.0
Havannah	1	A	50	66	H112CJ	*Pavona*	3.5966	0.0037	1.859	0.010	7.65	0.15	0.001305	0.000021	1.1502	0.0012	1.1502	0.0012	124.0	2.0	1898.3	3.2
Havannah	1	A	20	27	H112XCP	*Goniopora*	2.7292	0.0022	6.726	0.025	1.066	0.020	0.000868	0.000015	1.1469	0.0014	1.1470	0.0014	82.6	1.5	1980.0	11.0
Havannah	1	A	30	40	H112YCN	*Acropora*	3.6502	0.0033	3.520	0.029	3.619	0.093	0.001152	0.000022	1.1470	0.0012	1.1471	0.0012	109.7	2.1	1921.6	4.9
Havannah	1	B	270	436	H117AC	*Goniopora*	3.2649	0.0040	11.639	0.092	7.11	0.10	0.008342	0.000063	1.1445	0.0015	1.1449	0.0015	799.0	6.0	1286.0	16.0
Havannah	1	B	200	323	H117AQ	*Galaxea*	2.9403	0.0021	7.264	0.037	8.379	0.094	0.006835	0.000048	1.1470	0.0013	1.1473	0.0013	652.5	4.7	1410.0	12.0
Havannah	1	B	145	234	H117BD	*Galaxea*	2.9734	0.0024	1.215	0.006	34.01	0.35	0.004591	0.000028	1.1467	0.0013	1.1469	0.0013	438.0	2.7	1582.5	3.5
Havannah	1	B	75	121	H117BP	*Pavona*	3.7382	0.0031	9.692	0.024	3.597	0.042	0.003079	0.000032	1.1478	0.0013	1.1480	0.0013	293.3	3.1	1772.0	11.0
Havannah	1	B	15	24	H117CC	*Pocillopora*	2.3913	0.0023	0.825	0.004	4.414	0.077	0.000503	0.000009	1.1486	0.0014	1.1486	0.0014	47.8	0.9	1972.0	2.2
Havannah	2	A	195	367	H27AA	*Galaxea*	3.0543	0.0030	4.902	0.020	9.18	0.13	0.004852	0.000057	1.1473	0.0013	1.1476	0.0013	463.0	6.0	1581.4	9.0
Havannah	2	A	145	273	H27AJ	*Montipora*	3.7564	0.0034	5.421	0.022	5.80	0.10	0.002762	0.000041	1.1466	0.0013	1.1468	0.0013	263.3	3.9	1777.9	7.5
Havannah	2	A	45	85	H27AZ	*Goniopora*	2.7942	0.0031	2.563	0.007	3.586	0.088	0.001086	0.000026	1.1478	0.0015	1.1478	0.0015	103.4	2.5	1927.8	5.0
Havannah	2	A	70	132	H27X	*Goniopora*	2.7646	0.0023	27.82	0.18	1.038	0.017	0.003450	0.000039	1.1445	0.0013	1.1448	0.0013	329.7	3.7	1890.0	42
Havannah	2	A	100	188	H27Y	*Pavona*	3.8486	0.0037	16.862	0.063	2.208	0.026	0.003194	0.000029	1.1459	0.0014	1.1461	0.0014	304.8	2.8	1797.0	19.0
Havannah	2	B	360	413	H212AC	*Goniopora*	2.9623	0.0030	4.069	0.015	23.37	0.30	0.01057	0.00011	1.1459	0.0017	1.1464	0.0017	1012	10.0	1028.0	12.0
Havannah	2	B	225	258	H2154BD	*Alveopora*	2.9544	0.0026	1.546	0.003	30.37	0.43	0.005247	0.000072	1.1478	0.0013	1.1481	0.0013	500.3	6.9	1522.6	7.4
Havannah	2	B	140	161	H2154BX	*Goniopora*	2.8038	0.0021	16.294	0.075	1.97	0.06	0.003784	0.000097	1.1468	0.0012	1.1471	0.0012	360.9	9.3	1771.0	26.0
Havannah	2	B	90	103	H2154CF	*Pavona*	3.6151	0.0038	0.588	0.003	23.55	0.43	0.001265	0.000019	1.1448	0.0014	1.1448	0.0014	120.7	1.8	1894.0	2.1
Havannah	2	B	90	103	H2154CQ	*Goniopora*	2.8300	0.0025	30.435	0.250	0.942	0.036	0.00334	0.00011	1.1480	0.0014	1.1484	0.0014	319.0	10.0	1915.0	46.0
Havannah	2	B	45	52	H2154X	*Goniopora*	2.7397	0.0024	2.584	0.059	1.842	0.076	0.000574	0.000013	1.1464	0.0014	1.1464	0.0014	54.7	1.2	1977.0	4.6

Notes:
1. Measurements were corrected using ^{230}Th and ^{232}Th internal standards
2. Age calculations were corrected using the decay constants of Cheng et al. (2000).
3. Corrected ^{230}Th ages were calculated assuming a two-component mixing model for the non-radiogenic ^{230}Th: Component 1 - dissolved initial Th based on average measurements of live corals from Pandora and Havannah reefs which give non-radiogenic ^{230}Th/^{232}Th activity = 1.00 and ^{232}Th = 0.7 ppb. Component 2 - non- carbonate sediment contamination through post-mortem terrigenous sediment infiltration with non-radiogenic ^{230}Th/^{232}Th activity = 0.65 (value calculated from mean Th/U ratio of 4.8 +/-0.9 from ICP-MS analyses of over 40 sediments and dusts from the Burdekin River catchment area.

Table S2. Known ecological descriptions of the prominent genera of benthic foraminifers from Havannah and Pandora Reef, central GBR (data compiled from Murray, 2006). * Indicates information from this study.

Genera	Test structure	Life mode	Substrate	Feeding mode	Salinity	Temperature	Depth	Environment
Photosymbiont								
Alveolinella (Dinoflagellate symbiont)	Porcellaneous	Epifaunal, clinging	Algal-covered carbonate gravels	Herbivore, symbiont	Marine	18 - 28°C	5 - 100m	Inner shelf lagoon
Amphistegina (Diatom symbiont)	Hyaline	Epifaunal, free	Phytal, coarse carbonate	Herbivore, symbiont	Marine	15 - 20°C	0 - 130m	Lagoons and coral reefs
Calcarina (Diatom symbiont)	Hyaline	Epifaunal, free	Sediment	Herbivore, symbiont	Marine	18 - 26°C	0 - 5m	Lagoons, coral reefs, inner shelf
Baculogypsina (Diatom symbiont)	Hyaline	Epifaunal, clinging	Phytal	Herbivore, symbiont	Marine	>25°C	0 -10m	Coral reefs, lagoons
Elphidium (Retains chloroplasts)	Hyaline			Herbivore, symbiont	Marine	Tropical*	5m*	Inshore coral reef*
Heterostegina (Diatom symbiont)	Hyaline	Epifaunal, free	Muddy carbonate sediment and hard substrate	Herbivore, symbiont	Marine	18 - 26°C	0 - 130m	Shelf, lagoon, seeks shade
Marginopora (Dinoflagellate symbiont)	Porcellaneous	Epiphytic, attached	Phytal, carbonate sand and gravel	Herbivore, symbiont	Marine	18 - 26°C	0 - 45m	Inner shelf, coral reefs, lagoons
Operculina (Diatom symbiont)	Hyaline	Epifaunal, free	Carbonate sediment	Herbivore, symbiont	Marine	Warm	0 - 130m	Lagoon to shelf
Parasorites (Dinoflagellate symbiont)	Porcellaneous			Herbivore, symbiont	Marine	Tropical*	0 - 5m*	Inshore coral reef*
Peneroplis (Rhodophycean symbiont)	Hyaline	Epifaunal, clinging	Plants and hard substrate	Herbivore, symbiont	Marine - hypersaline	18 - 27°C	0 – 70m	Lagoons and inner shelf
Sorites (Dinoflagellate symbiont)	Porcellaneous	Epiphytic, clinging	Plants, especially seagrass	Herbivore, symbiont	Marine - hypersaline	18 - 26°C	0 – 70m	Lagoons and inshore reefs

Genera	Test structure	Life mode	Substrate	Feeding mode	Salinity	Temperature	Depth	Environment
Heterotrophic								
Ammonia	Hyaline	Infaunal, free	Muddy sand	Herbivore	Brackish - marine - hyersaline	Warm-tropical	0 - 50m	Inner shelf
Bigenerina		Epifaunal, free	Sediment	Omnivore	Marine	Temperate - warm	5m*	Shelf
Bolivina	Hyaline	Infaunal-epifaunal, free	Muddy sediment; can tolerate dysoxia	Detritivore	Marine	Cold-warm	0 - 500m	Inner shelf to bathyal
Clavulina	Agglutinated				Marine	Tropical*	5m*	Inshore coral reef*
Cymbaloporetta	Hyaline				Marine	Tropical*	5m*	Inshore coral reef*
Epistomaroides					Marine	Tropical*	5m*	Inshore coral reef*
Eponides	Hyaline	Epifaunal, free or clinging	Sediment or hard substrate	Detritivore	Marine	Cold	5m*	Shelf, abyssal
Hauerina	Hyaline				Marine	Tropical*	5m*	
Pararotalia		Epifaunal, free	Sand	Herbivore	Marine	Warm	5m*	Inner shelf
Pyrgo	Porcellaneous	Epifaunal, infaunal, free or clinging	Plants or sediment	Herbivore and Detritivore	Marine	Cold, temperate and warm	5m*	Innershelf, shelf to bathyal
Quinqueloculina	Porcellaneous	Epifaunal, free or clinging			Marine - hyersaline	Cold - warm	5m*	Hyposaline lagoons, midshelf and rarely bathyal
Spiroloculina	Porcellaneous	Epifaunal, free or clinging	Plants or sediment	Herbivore	Marine - hyersaline	Temperate - warm	0 - 40m	Lagoon, inner shelf
Sahulia	Agglutinated				Marine	Tropical*	5m*	Inshore coral reef*
Textularia	Agglutinated	Epifaunal, free or clinging	Hard substrate, sediment	Detritivores	Marine	Cold-warm	0 - 500m	Lagoons, shelf to bathyal

Table S3. Pairwise comparisons of Margalef richness (d') of foraminiferal communities between Pandora and Havannah Reef throughout the time series. The pairwise comparison was permutated under a full model using Euclidean distance and partial Type III sums of squares. Significance is indicated in bold when $p < 0.05$. To allow temporal replication among cores, 5 cm sub-samples were pooled into 50 yr bins (as defined by U-series chronology).

Margalef richness (d')		
[230]Th age (A.D.)	t	p
2010	0.468	0.628
1960	0.626	0.591
1910	0.125	0.889
1860	1.0549	0.304
1810	0.576	0.636
1760	0.701	0.512
1710	1.634	0.148
1660	0.485	0.621
1610	0.932	0.504
1560	0.493	0.672
1510	0.381	0.729
1460	4.831	**0.001**
1410	1.618	0.216
1360	0.534	0.504
1310	0.610	0.495
1260	10.007	**0.001**
1210	5.575	**0.001**

Table S4. Geochemical data for each sampled interval. Carbon stable isotope ratios are reported relative to the Pee Dee Belemnite (V-PDB) standard. Age and depth of the sample were calculated from the average accretion rate per core extrapolated from the TIMS U-Series analysis. Core ID has been abbreviated, the first letter refers to the site either Havannah (H) or Pandora (P), the number refers to the transect (1 or 2) and the last letter refers to the core (A or B).

| Core ID | ^{230}Th age (A.D.) | Core depth (cm) | % Content | | C:N (molar) | δ^{13}C (V-PDB) |
			C_{org}	N		
H1A	Modern	0-5	1.95	0.26	7.50	-18.7
H1A	1910	15-20	1.91	0.27	7.07	-17.8
H1A	1860	35-40	1.92	0.27	7.11	-17.5
H1A	1810	50-55	1.77	0.24	7.38	-17.7
H1A	1760	65-70	1.74	0.23	7.57	-18.3
H1A	1710	85-90	1.58	0.23	6.87	-17.9
H1A	1660	100-105	1.56	0.21	7.43	-17.8
H1A	1610	120-125	1.37	0.18	7.61	-17.4
H1A	1560	135-140	1.37	0.16	8.56	-17.8
H1A	1510	155-160	1.27	0.14	9.07	-18.0
H1A	1460	170-175	1.35	0.15	9.00	-18.1
H1A	1410	190-195	1.37	0.17	8.06	-17.7
H1A	1360	205-210	1.36	0.18	7.56	-18.0
H1A	1310	225-230	1.24	0.16	7.75	-18.3
H1A	1260	240-245	1.2	0.14	8.57	-18.2
H1A	1210	260-265	1.34	0.15	8.93	-19.2
H1A	1160	275-280	1.31	0.15	8.73	-18.1
H1A	1110	295-300	1.36	0.17	8.00	-19.0
H1A	1060	310-315	MD	MD	MD	MD
H1A	1010	325-330	1.08	0.13	8.31	-18.6
H1A	960	345-350	1.11	0.13	8.54	-18.4
H1A	910	360-365	1.5	0.16	9.38	-17.9
H1B	Modern	0-5	2.3	0.31	7.42	-18.5
H1B	1910	15-20	1.89	0.24	7.88	-18.0
H1B	1860	35-40	1.65	0.2	8.25	-17.8
H1B	1810	55-60	1.56	0.18	8.67	-18.1
H1B	1760	70-75	1.52	0.17	8.94	-18.1
H1B	1710	90-95	1.76	0.22	8.00	-17.6
H1B	1660	110-115	1.55	0.17	9.12	-18.1
H1B	1610	125-130	1.46	0.16	9.13	-18.4
H1B	1560	150-155	1.41	0.15	9.40	-18.3
H1B	1510	170-175	1.5	0.15	10.00	-18.3
H1B	1460	190-195	1.4	0.15	9.33	-17.3
H1B	1410	205-210	1.49	0.15	9.93	-18.5
H1B	1360	225-230	1.26	0.13	9.69	-18.7
H1B	1310	245-250	1.42	0.15	9.47	-18.7
H1B	1260	260-265	1.37	0.14	9.79	-18.7
H1B	1210	280-285	1.41	0.15	9.40	-19.4
H2A	Modern	0-5	1.69	0.26	6.50	-18.1
H2A	1910	20-25	1.88	0.25	7.52	-18.1
H2A	1860	45-50	1.63	0.22	7.41	-17.7
H2A	1810	65-70	1.77	0.23	7.70	-17.8
H2A	1760	90-95	2.05	0.24	8.54	-19.3
H2A	1710	110-115	1.66	0.19	8.74	-17.8
H2A	1660	135-140	1.63	0.19	8.58	-17.6

H2A	1610	155-160	1.49	0.18	8.28	-17.9
H2A	1560	180-185	1.61	0.18	8.94	-17.8
H2A	1510	195-200	1.5	0.17	8.82	-18.2
H2B	Modern	0-5	1.51	0.17	8.88	-17.7
H2B	1910	15-20	1.45	0.18	8.06	-18.1
H2B	1860	35-40	1.63	0.25	6.52	-18.4
H2B	1810	55-60	1.49	0.21	7.10	-18.3
H2B	1760	75-80	1.49	MD	MD	-19.6
H2B	1710	90-95	1.36	0.17	8.00	-16.9
H2B	1660	110-115	1.6	0.21	7.62	-19.1
H2B	1610	130-135	1.42	0.17	8.35	-18.6
H2B	1560	155-160	1.55	0.2	7.75	-22.6
H2B	1510	170-175	1.4	0.13	10.77	-24.0
H2B	1460	190-195	1.36	0.12	11.33	-23.2
H2B	1410	210-215	1.29	0.13	9.92	-22.9
H2B	1360	230-235	1.25	0.14	8.93	-18.2
H2B	1310	245-250	1.37	0.17	8.06	-22.6
H2B	1260	265-270	1.47	0.17	8.65	-19.8
H2B	1210	285-290	1.58	0.19	8.32	-18.6
H2B	1160	305-310	1.47	0.17	8.65	-17.9
H2B	1110	320-325	1.36	0.14	9.71	-19.0
H2B	1060	340-345	1.49	0.19	7.84	-18.4
H2B	1010	360-365	1.48	0.15	9.87	-19.1
H2B	960	380-385	1.63	0.18	9.06	-18.9
P2A	Modern	10-15	2.11	0.21	11.90	-12.7
P2A	1910	35-40	1.33	0.09	17.10	-11.9
P2A	1860	60-65	1.36	0.11	14.40	-11.8
P2A	1810	90-95	1.2	0.09	16.30	-12.0
P2A	1760	115-120	1.27	0.1	14.20	-12.1
P2A	1710	140-145	1.24	0.09	16.60	-12.3
P2A	1660	170-175	1.32	0.09	16.80	-12.0
P2A	1610	195-200	1.25	0.08	17.80	-12.5
P2B	Modern	0-5	1.81	0.19	11.30	-12.0
P2B	1910	25-30	1.21	0.1	13.70	-11.5
P2B	1860	85-90	1.22	0.13	10.60	-11.6
P2B	1810	145-150	1.12	0.09	15.30	-12.2
P2B	1760	200-205	1.34	0.08	20.80	-12.8
P2B	1710	260-265	1.13	0.09	14.70	-12.1
P2B	1660	315-320	1.28	0.08	19.90	-13.0
P3A	Modern	0-5	1.77	0.18	11.40	-11.9
P3A	1910	20-25	1.52	0.11	16.20	-10.9
P3A	1860	40-45	1.47	0.11	15.70	-11.4
P3A	1810	60-65	1.62	0.12	15.60	-10.8
P3A	1760	80-85	1.58	0.11	16.70	-11.9
P3A	1710	100-105	1.4	0.1	17.00	-11.1
P3A	1660	120-125	1.4	0.11	15.30	-11.4
P3A	1610	140-145	1.43	0.08	20.30	-12.4
P3A	1560	160-165	1.35	0.1	16.50	-11.5
P3A	1510	180-185	1.55	0.11	16.50	-10.8
P3A	1460	200-205	2.09	0.13	18.20	-11.5
P3A	1410	220-225	2.21	0.13	19.60	-13.1
P3A	1360	240-245	1.52	0.07	25.80	-12.2
P3A	1310	260-265	1.77	0.09	22.90	-12.6
P3A	1260	280-285	1.07	0.05	25.90	-13.0
P3A	1210	295-300	1.17	0.07	20.10	-12.2
P3B	Modern	0-5	1.83	0.23	9.30	-11.4
P3B	1910	20-25	1.55	0.16	11.00	-10.8
P3B	1860	45-50	1.5	0.16	10.90	-10.3
P3B	1810	75-80	1.64	0.16	12.20	-11.1

P3B	1760	100-105	1.9	0.19	11.60	-11.2
P3B	1710	125-130	3.21	0.27	14.60	-19.5
P3B	1660	150-155	1.66	0.16	12.30	-11.8
P3B	1610	180-185	1.32	0.11	13.80	-11.8
P3B	1560	205-210	1.84	0.17	12.50	-11.2
P3B	1510	230-235	2.22	0.19	13.90	-11.9
P3B	1460	255-260	1.82	0.13	16.30	-12.7
P3B	1410	280-285	2.02	0.16	14.40	-13.6
P3B	1360	310-315	2.85	0.23	14.30	-13.0

*MD= Missing data

Table S5. Pairwise comparisons of the average C:N values between Pandora and Havannah Reef throughout the time series. The pairwise comparison was permutated using Euclidean distance and partial Type III sums of squares. Significance is indicated in bold when $p < 0.05$. To allow temporal replication among cores, 5 cm sub-samples were polled into 50 yr bins (as defined by U-series chronology).

	C:N	
^{230}Th age (A.D.)	t	p
2010	5.012	**0.001**
1960	2.858	**0.001**
1910	3.246	**0.021**
1860	3.541	**0.001**
1810	2.042	0.115
1760	4.540	**0.001**
1710	5.568	**0.001**
1660	3.634	**0.001**
1610	4.495	**0.001**
1560	2.363	0.117
1510	2.196	0.189
1460	4.419	0.110
1410	2.192	0.099
1360	2.603	0.099
1310	20.247	**0.001**
1260	9.610	**0.001**
1210	138.950	**0.001**

Supplementary material References

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Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Melbourne.

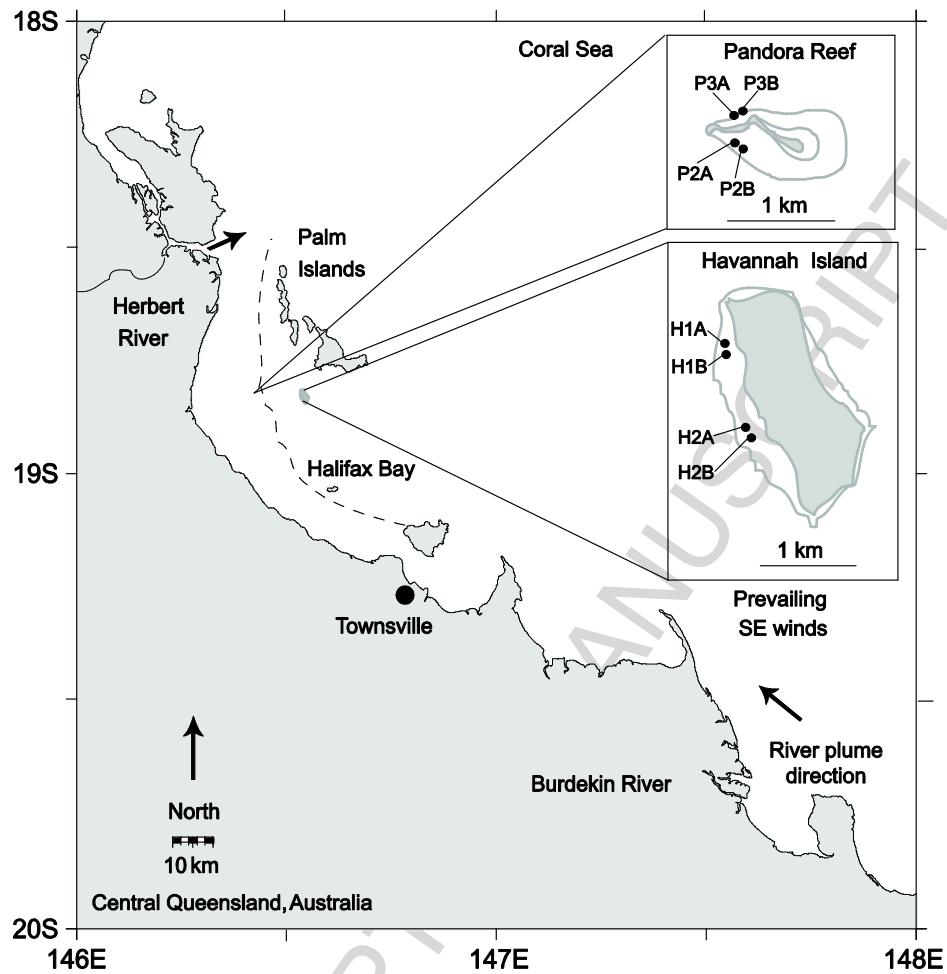Roff, G., 2010. Historical ecology of coral communities from the inshore Great Barrier Reef. PhD thesis, The University of Queensland. UQ eSpace. 138 pp.
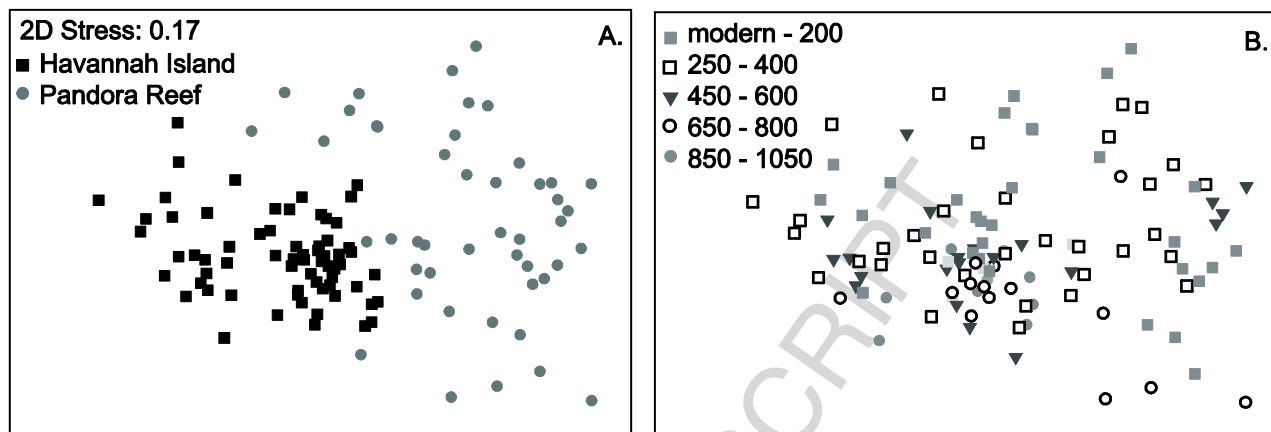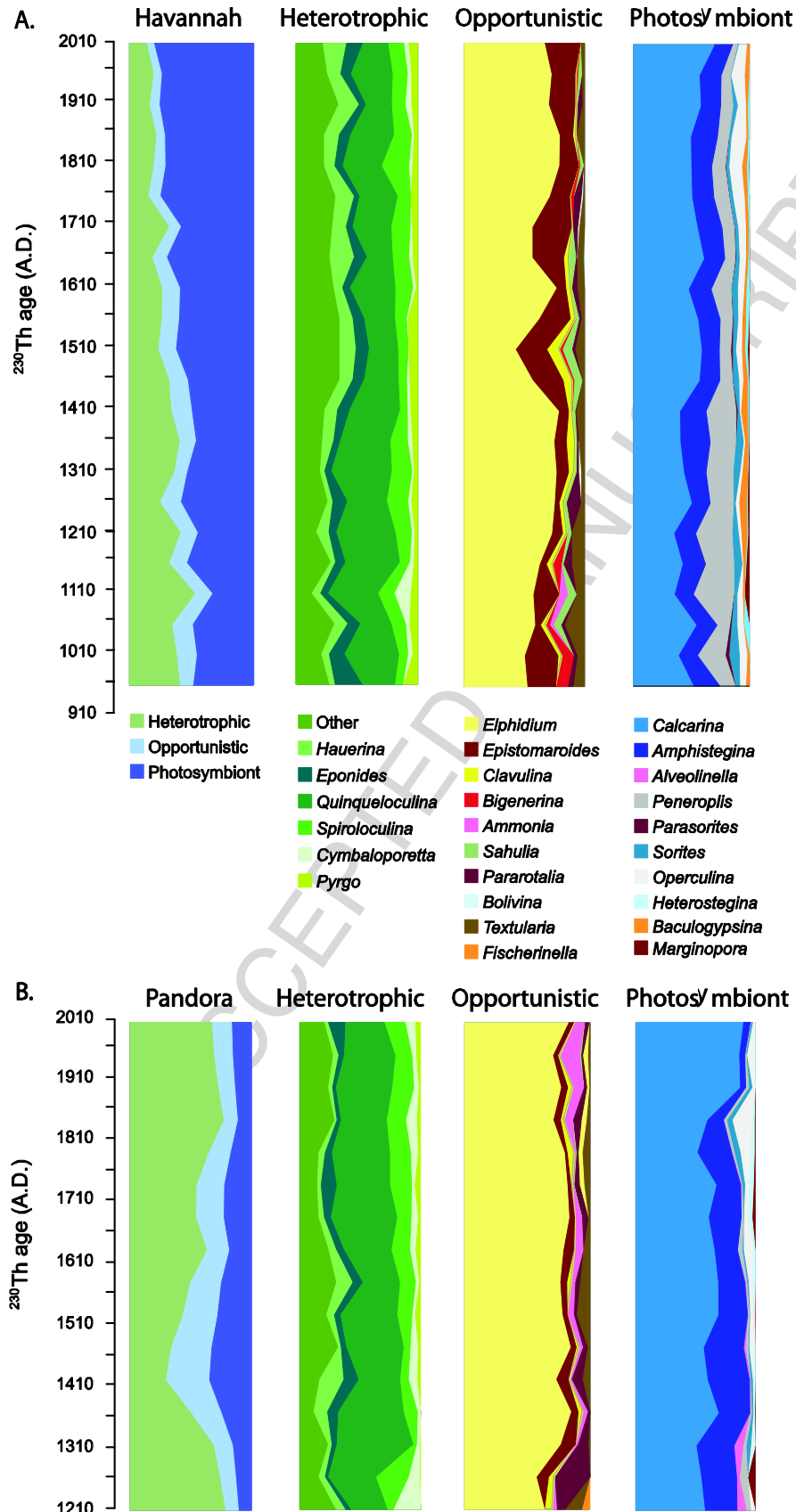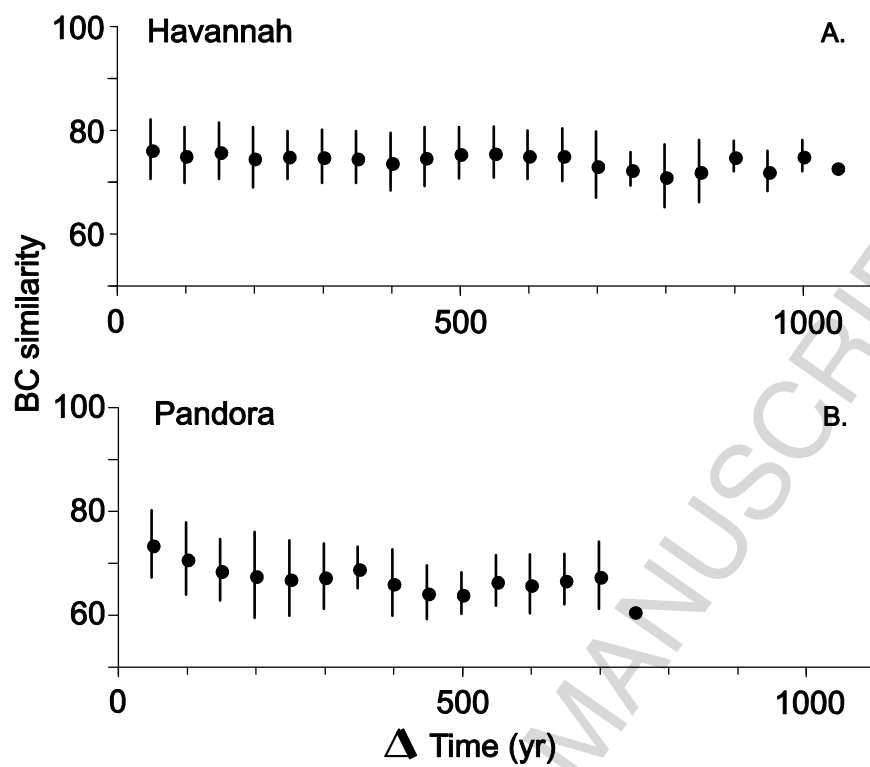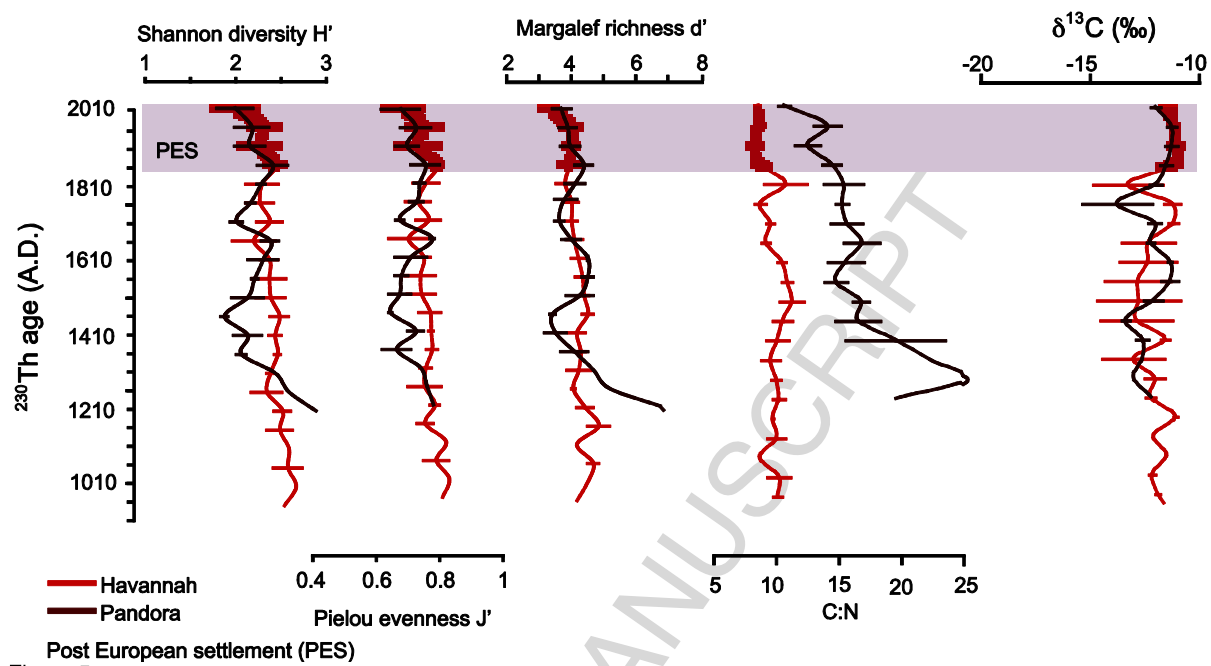
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Highlights for Reymond et al Research Article:

1. Foram communities show greater spatial than temporal variability over millennial time scales.

2. Diversity was high regardless of the functional groups or geochemical signature.

3. The distribution of functional groups correlates with the amount of sedimentary organic matter.

4. Geochemical proxies indicate long-term catchment runoff from terrestrial sources.