Ecological incumbency impedes stochastic community assembly in Holocene foraminifera from the Huon Peninsula, Papua New Guinea

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Abstract.—Persistence in the structure of ecological communities can be predicted both by deterministic and by stochastic theory. Evaluating ecological patterns against the neutral theory of biodiversity provides an appropriate methodology for differentiating between these alternatives. We traced the history of benthic foraminiferal communities from the Huon Peninsula, Papua New Guinea. From the well-preserved uplifted reef terrace at Bonah River we reconstructed the benthic foraminiferal communities during a 2200-year period (9000–6800 yr B.P.) of reef building during the Holocene transgressive sea-level rise. We found that the similarity of foraminiferal communities was consistently above 60%, even when comparing communities on either side of a massive volcanic eruption that smothered the existing reef system with ash. Similarly, species diversity and rank dominance were unchanged through time. However, similarity dropped dramatically in the final stages of reef growth, when accommodation space was reduced as sea-level rise slowed. We compared the community inertia index (CII) computed from the observed species abundances with that predicted from neutral theory. Despite the differences in foraminiferal community composition in the younger part of the reef sequence, we found an overall greater degree of community inertia with less variance in observed communities than was predicted from neutral theory, regardless of foraminiferal community size or species migration rate. Thus, persistent species assemblages could not be ascribed to neutral predictions. Ecological incumbency of established foraminiferal species likely prevented stochastic increases in both migrant and rare taxa at the Bonah River site. Regardless of the structuring mechanisms, our reconstruction of Holocene foraminiferal assemblages provides historical context for the management and potential restoration of degraded species assemblages.

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Introduction

One of the most important ecological questions is the relative extent to which ecological communities are structured by stochastic (Gleason 1926) versus deterministic processes such as niche partitioning (Elton 1927; Chase and Leibold 2003). The recent development of the neutral theory of biodiversity (Hubbell 1997, 2001; Volkov et al. 2003, 2005) has allowed the question of community organization to be revisited with the use of an appropriate null model. Some studies have been carried out in the fossil record, with purported examples of both niche-based (Pandolfi 1996) and stochastic interpretations (Olszewski and Erwin 2004; Holland and Patzkowsky 2004). One source of confusion in attempts to test the relative influence of stochastic versus deterministic explanations for community structure has been that both neutral and niche theory predict high levels of similarity among ecological communities over broad spatial and temporal scales (McGowan and Walker 1985; Brett et al. 1995, 1996; Morris et al. 1995; Boucot 1996; Pandolfi 1996, 2002; DiMichele et al. 2004; McGill et al. 2005), though lack of such similarity has usually been taken as a sign that stochastic demographic influences (i.e., neutral processes) dominate community dynamics (Miller 1988; Lafferty and Miller 1994; Patzkowsky 1995; Bonuso et al. 2002).

The raised sea cliffs from the Huon Peninsula, Papua New Guinea, spectacularly preserve coral reef assemblages that lived in

shallow subtidal habitats of coastal fringing reefs throughout the transgressive phase of reef growth during the mid to late Holocene (Chappell 1974, 1983; Chappell and Polach 1991; Pandolfi and Chappell 1994). Alongside the fossilized remains of corals lie prolific numbers of benthic foraminifera (shelled protists), whose diversity matches that of the reef-building corals. The Holocene sequence allows historical observation of foraminiferal assemblages on the scale of hundreds of years (Pandolfi et al. 2006). Such scales are intermediate between the seasonal to decadal short-term cyclic dynamics of living ecological communities, ubiquitous in modern ecological data sets, and older paleoecological time series that lack the resolution required to observe finer nuances of ecological patterns characteristic of shorter intervals.

We investigated the community structure of Holocene foraminiferal assemblages over a ~2200-year interval from a single reef. The communities were subjected to two different kinds of disturbances. A ''press'' disturbance (Connell 1997) occurred over hundreds of years when the sea-level rise slowed during the waning phases of the Holocene transgression (7000–6000 yr B.P.). A ''pulse'' (Connell 1997) disturbance occurred instantaneously at the study site around 8750 yr B.P. when a volcanic eruption resulted in the mass mortality of coral communities over a 16-km stretch of Huon coastline, including the Bonah River reef (Pandolfi et al. 2006). Our first question concerns the degree to which communities varied over the contrasting time scales of these disturbances, and the potential role of ecological incumbency in maintaining persistent community structure. Our second question concerns whether the neutral model can explain foraminiferal community similarity through time, as evaluated by calculating the community inertia index (CII), developed in McGill et al. (2005), and comparing it with neutral expectations.

Methods

Study Site.—The island archipelago of New Guinea, located about 150 km north of Australia, lies in the western Pacific Ocean where reef coral diversity is greatest (Connolly
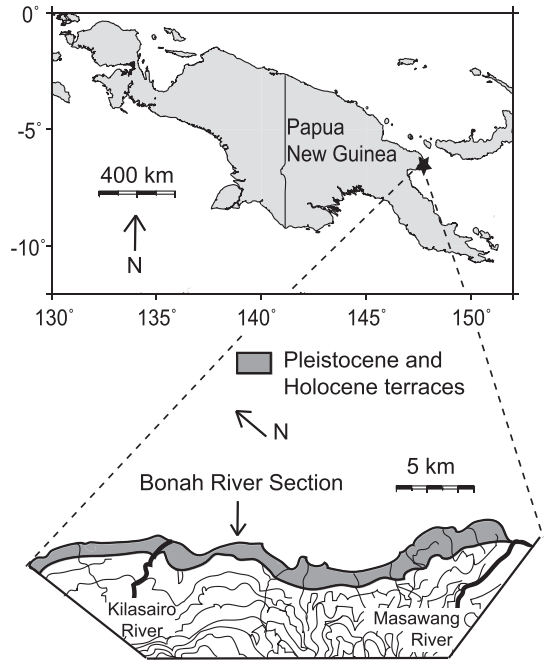

FIGURE 1. Map of study area in Papua New Guinea (PNG) showing the location of the Huon Peninsula (star). Each section on the dashed scale bar represents 100 km. Below is a topographical map of the Huon Peninsula coastline. The Bonah River section is located at 6°10.4598′S latitude and 47°40.0110′E longitude.

et al. 2005) and conditions for reef development are optimal. The region is actively undergoing tectonism and, along the Huon Peninsula coast, this has resulted in the uplift of a spectacular set of fossilized terraces built mainly from raised coral reefs (Fig. 1) (Chappell 1974; Pandolfi and Chappell 1994). Here, human population density is uniformly low, and this has been the case for the past 40,000 years (Groube et al. 1986). The present climate is broadly similar to that of the Holocene, with a seasonal sea-surface temperature range of 2°C around a 29°C mean, few major storms, and no cyclones. Compared to the present, the El Niño-Southern Oscillation inter-annual variability was reduced in the Holocene (Tudhope et al. 2001).

The Holocene geo-biological system at Huon Peninsula provides an exceptional opportunity to study paleoecological patterns in coral reefs. During a sustained sea-level rise of the last deglaciation, shallow-water reef deposits containing foraminifera and diverse coral reef assemblalages grew between 11,000 and

6400 yr B.P. (Pandolfi et al. 2006). Reef growth during this period was continuous and "kept up" (Neumann and Macintyre 1985) with the most recent post-glacial sea-level rise, averaging up to 10 m of reef growth per 1000 years (Chappell and Polach 1991).

The numerous streams, embayments, and sea cliffs that cut through the Holocene terrace expose a complete three-dimensional view of Holocene reef growth, geometry, and geography. The exposed uplifted sea cliffs of up to 24 m high preserve the former biological inhabitants, paleoecological history, and physical environments from shallow fore-reef slope, barrier reef crest, back reef, and lagoon environments. For example, most Holocene corals are found upright, whole, and in life position (Edinger et al. 2007). In this study we report on the foraminiferal assemblages from the shallow reef-crest habitat from the emerged Holocene sea cliffs adjacent to the Bonah River (Fig. 1).

We previously documented a volcanic eruption that occurred between 9 Ka and 8.6 Ka (Pandolfi et al. 2006). This major disturbance is evident from a clear layer of ash found within the layers of reef sediment at Bonah River. The volcanic ash smothered the living communities, creating a localized mass-mortality event. A mortality event of this kind affected the shallow reef-crest habitat only once in the 2200-year interval at Bonah River, suggesting that events of this magnitude are quite rare (Pandolfi et al. 2006). This event provides an opportunity to examine foraminiferal community structure directly before and after the large-scale "pulse" disturbance. The section at Bonah River also continues to the waning stages of reduced sea-level rise associated with the end of the Holocene transgression that had persisted since the Last Glacial Maximum.

Sampling and Preparation.—We collected three bulk samples along each of seven 25-m-long horizontal transects, laid at 1-m intervals vertically from the base to the top of the cliff at Bonah River (Fig. 1). We collected two bulk samples from an additional "basal" transect (below the volcanic ash), resulting in a total of 23 bulk-sediment samples from eight transects, representing eight separate time intervals. Bulk samples filled a calico sample bag of 10″ × 17″ (25.4 × 43.2 cm) and typically weighed ~2 kg. To achieve a representative subsample, we first split the 23 bulk samples in half. One half was returned to storage at the Marine Palaeoecology Laboratory, University of Queensland, Australia and the other half was split again. This process continued until a 100-gram sample remained. We collected the first 200 sighted benthic foraminifera from each of the 23 sediment samples from the 0.125 mm to 0.5 mm size class and identified them to species level. We used scanning electron microscope photographs to examine subtle morphological differences among species. Voucher specimens for each species have been deposited at the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (RGM 566008-566207). Several pristine coral samples from each transect were radiometrically age-dated by using ^{14}C at the NSF-University of Arizona AMS facility (Edinger et al. 2007). The eight transects range in age from 9 to 6.8 Ka.

Our analysis is restricted to only a single sampling locality (Bonah River), but we followed a hierarchical design for replicate samples along each horizontal transect (i.e., each time period). The analog would be three deep-sea cores within 25 m of each other in the Deep Sea Drilling Project (DSDP), where important information on the evolution of foraminifera has been gathered (Malmgren and Kennett 1981). However, our results apply only to a single reef and cannot be generalized further. Nonetheless, we anticipate that the results of this study will provide hypotheses that can be further evaluated by using the multiple sites we have sampled along the Huon Peninsula and elsewhere.

Data Analysis.—We reconstructed the community structure of benthic foraminiferal communities from species relative abundance data from the fossil assemblages. Histograms of raw abundance based on the top ten ranked species for the pooled samples were constructed for each of the eight time periods. To gain information on species diversity, we used two diversity metrics and species rank abundance plots.

We used Bulla's (1994) evenness (*E*), because it is considered to be the least biased and most robust and stable diversity index

(Mouillot and Wilson 2002). We used Bulla's diversity index (D) for consistency, because Bulla's evenness is used to calculate this diversity value. The Bulla evenness (1) and diversity (2) formulae are

$$E = \sum_{i=1}^{s} \min(p_i, 1/S) \qquad (1)$$

$$D = E \times S \qquad (2)$$

where S is the species number, p_i is the frequency of the ith species, E is Bulla's evenness, and D is Bulla's diversity. We used one-way ANOVA (calculated using STATISTICA, version 7 [Stat-Soft, Inc. 2004]) to examine differences in E and D through time, and then constructed plots of E and D through time. Cochran's test of homogeneity of variance was not significant for either diversity index, so the data complied with the assumption of a normal distribution. Species rank abundance plots were also used as a measure of diversity through time, to summarize both equitability in abundance among species and species richness.

We used the abundance of each species in each sample to calculate the Bray-Curtis (BC) similarity index (Bray and Curtis 1957) between all pairs of samples in the time series. Before calculating the BC index, we transformed the raw abundance data to the fourth root and standardized them in order to equalize the potential contribution of each species (Somerfield and Clarke 1995). To investigate variation in taxonomic composition among the different times we used an analysis of similarity (ANOSIM) (Clarke and Green 1988), a nonparametric test (analogous to ANOVA) that does not assume a normal distribution or a constant variance among the groupings (Clarke and Warwick 1994). The statistical test (Global R) for ANOSIM compares the observed differences among transects to differences among replicates within transects (Clarke and Green 1988). The nonmetric multidimensional scaling (NMDS) ordination is a visual representation of the BC community similarity. NMDS ordinations were used to graphically represent differences among foraminiferal communities from different times. A hierarchical cluster analysis on the similarity matrix was performed using the group average cluster method. We used the statistical package PRIMER version 6.1.5 (2006) to conduct the ANOSIM, NMDS ordinations, and cluster analysis.

A Mantel test (Mantel 1967) was used to test the relationship between the amount of time separating two samples and their taxonomic similarity (BC index). The sample statistic (*Rho*) is calculated by using the Spearman rank-correlation parameter between the observed time-separation and similarity. For this test we used the same BC community similarity matrix as in the ANOSIM and NMDS analyses, but compared it with an additional matrix containing the amount of time separating the samples. The two matrices (time and BC index) were then permutated 999 times using a randomization technique, which reorders the values of one matrix with the corresponding value in the second matrix (Sokal and Rohlf 1995). The correlation values of the randomized data generate an expected distribution that is compared with the sample statistic (*Rho*). If the observed measure of *Rho* is sufficiently different from the randomized distribution, then an association between the two matrices is accepted. In other words, if the sample statistic does not lie within the 95% bounds of the randomized distribution, we assume that time elapsed has a significant relationship with community similarity. The Mantel test was carried out in the software package PRIMER, using the subroutine RELATE (Somerfield et al. 2002).

The tendency for the set of species in an ecological community to recur with the same relative abundances is known as "community inertia" (McGill et al. 2005). The community inertia index (CII) was developed to help differentiate patterns in species distributions that imply deterministic processes governing community structure from those that imply unpredictable or random factors (McGill et al. 2005). Community inertia is measured by the rate of change of the BC similarity metric between temporally spaced samples from a single location. Although numerous metrics have been used to quantify similarity among communities (Bray and Curtis 1957; Bulla 1994; Somerfield et al. 2002), only the CII has

been compared with a null expectation (McGill et al. 2005). We follow McGill et al. (2005) in using neutral theory (Bell 2000; Hubbell 2001) to calculate the null expectation for community inertia. A spatially explicit neutral model is used to simulate the community changes we would expect to observe in an ecosystem driven only by demographic stochasticity (Gotelli and Ellison 2004). We derived expected neutral CII values following the methods outlined in McGill et al. (2005). Specifically, our neutral model comprises 50 local communities, each containing 1000 individuals—a metacommunity total of $J = 50,000$ individuals. Each local community was initially seeded with species found on the Huon Peninsula, randomly sampled from the first observed community, with replacement. Individuals die sequentially, and are replaced by the offspring of another individual selected at random from the metacommunity. These replacement dynamics assume that the neutral migration parameter is $m = 1.0$ (the highest possible value m can take, corresponding to "panmixia"), so our neutral model is equivalent to the single contiguous population used in McGill et al.'s (2005) CII analyses. If other factors are constant, neutral metacommunities with panmixic migration exhibit the highest levels of community inertia (McGill et al. 2005). Therefore, if the observed foraminiferal communities have a higher degree of community inertia than panmixic neutral analogs, it follows that observed community inertia is greater than the neutral model can generate for any value of m. Neutral dynamics are simulated over a 2500-year period, with each individual in the metacommunity being replaced annually. Both the fossil foraminiferal communities and their neutral analogs consisted of samples of 200 individuals, taken from the local communities at different time intervals to yield a trend in community similarity over time (we sampled the neutral communities at uniform 100-year intervals).

We calculated the BC similarity index for each pairwise comparison between time intervals, at each local community (as before, we normalized to the fourth root of the raw abundance data). We then fit the relationship between similarity and time difference between samples using a linear regression, for both neutral and observed metacommunities. The gradients of these fits measure the rate at which community composition changes through time—the community inertia index. A CII value of zero reflects an invariant community structure; negative CII values indicate a community whose structure becomes more dissimilar as time passes (McGill et al. 2005). For comparison with patterns from Quaternary mammals (McGill et al. 2005) we also calculated CII based on a Pearson correlation matrix. Because it is unclear how large the foraminiferal metacommunity is, we calculated the CII for increasingly large metacommunities (as J increases), again using the neutral theory (Hubbell 2001) as the ecological null model (Gotelli and McGill 2006). We used these data to assess whether our results are robust to the assumption of metacommunity size.

Results

A total of 81 species from 54 genera were obtained from 4600 individuals from 23 samples in eight time periods between 9 and 6.8 Ka at Bonah River, Papua New Guinea (PNG) (Table 1 in Supplementary Material online at Dryad: doi:10.5061/dryad.st1s3). The number of species found in each time period ranged from 37 to 50. There were no significant differences among the foraminiferal assemblages in their species diversity or evenness throughout the eight time intervals spanning 2200 years (Table 1, Fig 2). Species rank abundance plots also show a remarkable degree of consistency throughout the sequence (Fig. 3). Histograms of raw abundance (pooled within time) show several species that were commonly distributed throughout the Bonah River section, e.g., *Triloculina sommeri* and *Quinqueloculina crassicarinata* (Fig. 4).

Patterns in abundance through time vary among the three functional groups (Fig. 5). Small miliolid and perforate foraminifera are uniformly abundant throughout the sequence and agglutinated forms are uniformly rare (Fig. 5A). However, the abundance of symbiont-bearing miliolids and rotalids

TABLE 1. ANOVA summary table of Bulla diversity (D) and evenness (E) indices for foraminiferal communities from eight time periods in the Holocene Bonah River section from the Huon Peninsula, Papua New Guinea.

Index	Effect	Sum sq.	Mean sq.	$F_{(7,15)}$	p
Bulla diversity (D)	Transect age	44.59	6.37	0.84	0.57
Bulla evenness (E)	Transect age	0.01	0.002	1.05	0.44

steadily increases throughout the bulk of the sequence, with younger transects having a higher abundance of symbiont-bearing species such as *Peneroplis planatus* and *Elphidium striatopunctatum* (Fig. 5B). Even though the opportunistic species contributed a small proportion of the overall composition, a general decrease in abundance throughout the younger sections is apparent in species such as *Siphogenerina striatula* and *Rectobolivina cocosensis* (Fig. 5C).

FIGURE 2. Bulla diversity (A) and evenness (B) indices (mean ± standard error) through time from Holocene foraminiferal communities from the Huon Peninsula, Papua New Guinea. See Table 1 for ANOVA.

Both the NMDS ordination and the group cluster analysis showed two groups separated at 60% similarity, with one group containing the three replicate samples from the youngest transect and the other group containing all samples from the seven underlying transects (Fig. 6). Consistent with the NMDS and the cluster analysis, the taxonomic composition of foraminiferal communities varied significantly through time (ANOSIM test, $r = 0.396$, $p = 0.001$). The Mantel test showed a significant inverse relationship between community similarity and time separating the fossil assemblages (Table 2, $rho = 0.387$, $p = 0.001$), indicating that communities more separated in time were more different in their species composition.

Over the >2000-year interval, the observed communities maintain a greater degree of similarity (BC similarity ~0.60–0.82) than simulated neutral communities (BC similarity ~0.07–0.98). Initially the mean similarity for communities generated by the neutral model was higher than for the observed communities (for communities separated by <590 years), but it decreased below the observed similarity for communities separated by longer time intervals (Fig. 7). The community inertia index (CII, based on the rate at which the BC similarity changes) calculated from the observed communities is negative, and very small, indicating that the foraminifera communities display considerable community inertia (CII, measured by the linear regression slope $= -1.2 \times 10^{-5}$, 95% CI $= [-2.3 \times 10^{-5}, -2.5 \times 10^{-7}]$) (Fig. 7). The CII of the analogous neutral communities is 20 times larger, indicating that we would expect to see much less inertia if the foraminifera community dynamics were driven by demographic stochasticity alone (slope $= -2.7 \times 10^{-4}$, 95% CI $= [-2.7 \times 10^{-4}, -2.71 \times 10^{-4}]$) (Fig. 7).

The community size for benthic foraminifera is difficult to estimate, so we calculated the CII for a range of metacommunity sizes, to
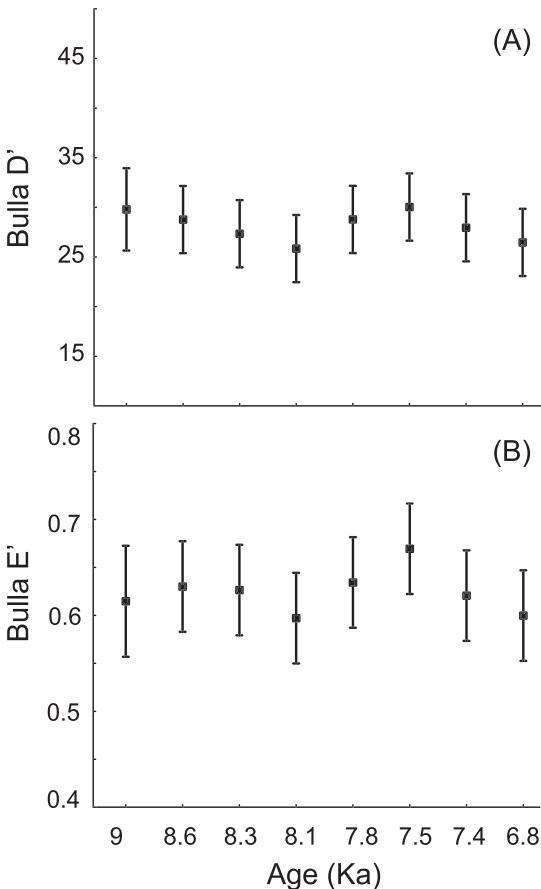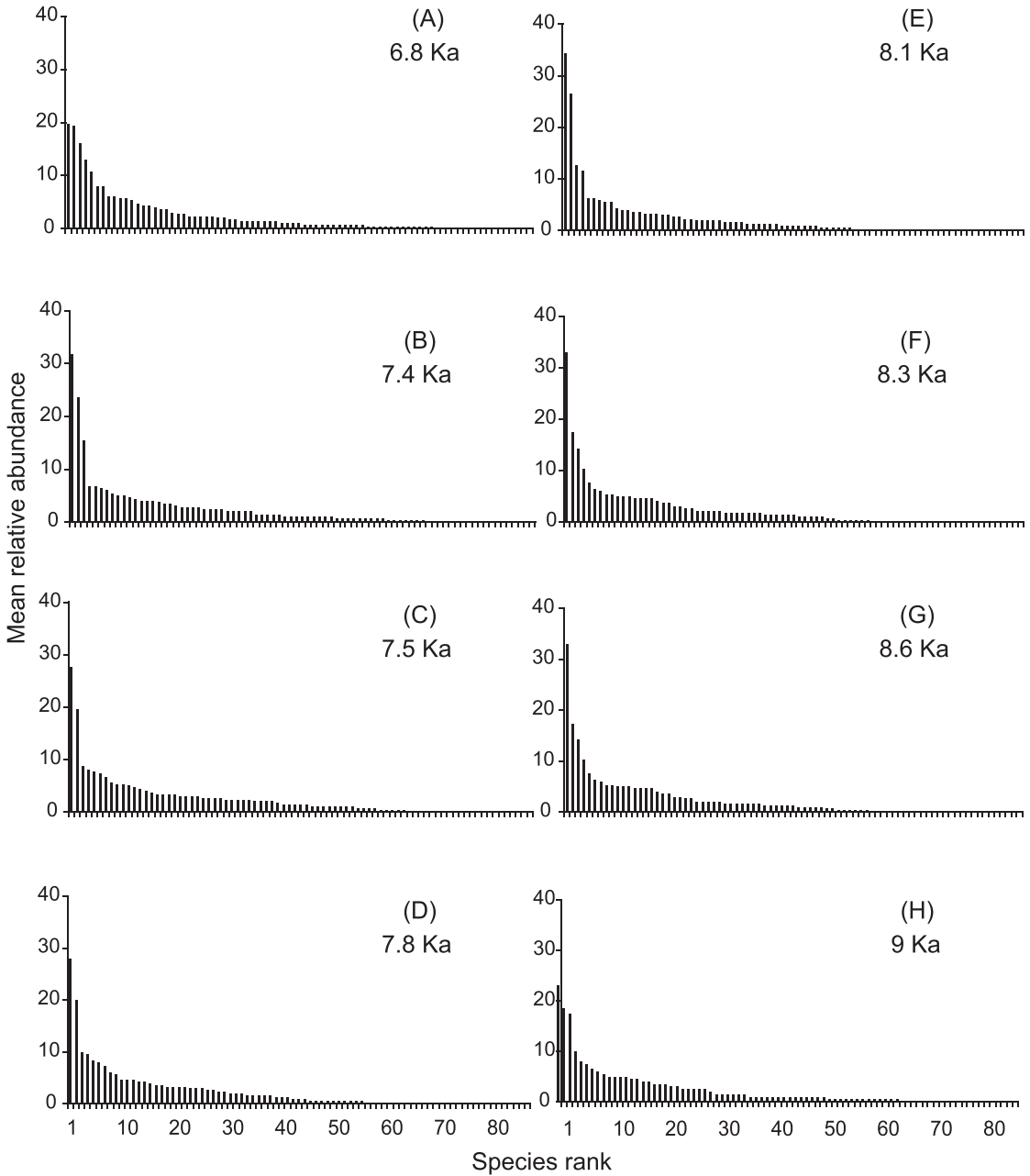
FIGURE 3. Species rank abundance plots for 81 species of Holocene foraminifera from the Huon Peninsula, Papua New Guinea, ordered from the youngest (A) to the oldest (H) transect. Mean relative abundance values for each species are the average of multiple (two or three) samples within each of the eight time periods.

assess whether a larger neutral metacommunity could better reflect observed foraminiferal community inertia. Plots of the log-transformed CII against community size verify that neutral communities change faster than the observed foraminiferal communities, and that this discrepancy could not be resolved by larger metacommunities (Fig. 8). If we fit the change in CII gradient with increasing metacommunity size by using a negative exponential curve, the high inertia found in the observed foraminiferal communities cannot be recreated by neutral communities for any value of J (Fig. 8).
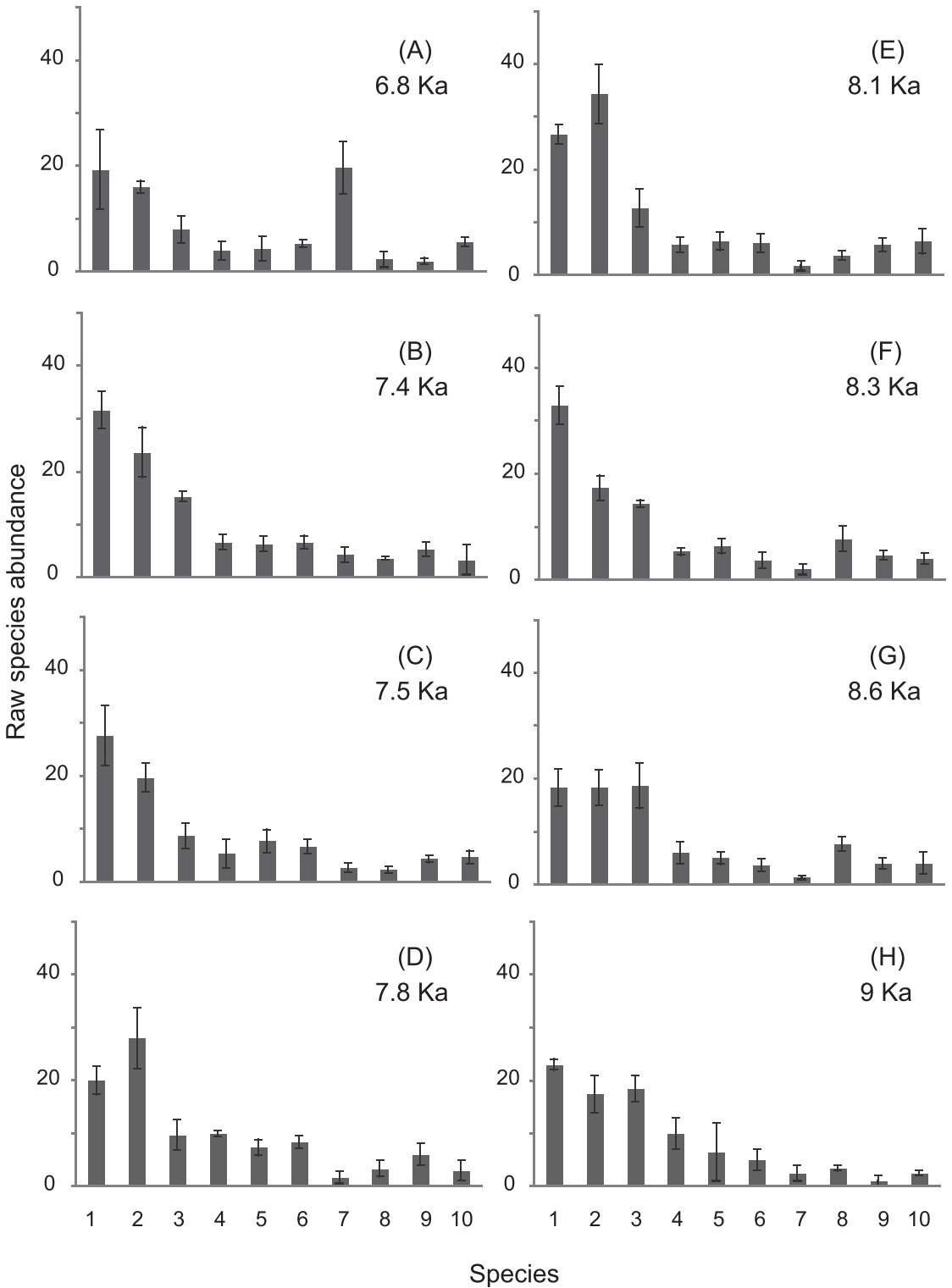
FIGURE 4. Histograms, ordered from the youngest (A) to the oldest (H) transect, of the top ten species contributing to the pooled abundance from the eight transects (mean ± standard error). The values on the y-axis are the raw species abundances, derived from 200 individuals from each of two or three samples per transect. The x-axis labels correspond to the following species: 1, *Triloculina sommeri*; 2, *Quinqueloculina crassicarinata*; 3, *Siphogenerina striatula*; 4, *Miliolinella labiosa*; 5, *Rosalina globularis*; 6, *Cymbaloperotta bradyi*; 7, *Eponides repandrus*; 8, *Rectobolivina cocosensis*; 9, *Quinqueloculina bassensis*; 10, *Quinqueloculina philippensis*.

Discussion

Foraminifera Species Distribution Patterns

From the 81 species of benthic foraminifera found from the Bonah River Holocene reef section, heterotrophic miliolids were the most abundant, constituting 62% of the overall foraminiferal abundance. The top ten common species comprised epifaunal small miliolids (*Triloculina sommeri, Quinqueloculina crassicarinata, Q. bassensis, Q. philippensis,* and *Millolinella labiosa*), epifaunal opportunistic species (*Siphogenerina striatula* and *Rectobolivina cocosensi*), epifaunal small perforated rotaliina (*Rosalina globularis*), epiphytic small perforated rotaliina (*Cymbaloperotta bradyi*), and small non-perforated rotaliina (*Eponides repandus*) (Fig. 4). Our study documents a highly diverse assemblage of foraminifera that lived in the shallow subtidal waters along the fringing reefs of coastal Huon Peninsula throughout the Holocene transgressive phase of reef growth.

The common foraminifera from the Bonah River section show both global distribution patterns and wide environmental tolerances. Modern-day assemblages of three of the Bonah River miliolids, *Q. philippinensis, Q. bassensis,* and *M. labiosa*, have been reported from a broad bathymetric range and are associated with a variety of reef biotopes (Haig 1988; Venecpeyre 1991). Among the other miliolids, *Q. crassicarinata* is found in both inshore and offshore reefs (Debenay 1988; Haig 1993), and *M. labiosa* is reported from reef lagoons (Javaux 1999), the back reefs of the Belize shelf (Wantland 1975), and mangrove swamps in Barbuda (Brasier 1975). *Triloculina* includes numerous species with highly variable distributions, but is mainly reported from lagoons, reefs, and their associated environments (Javaux and Scott 2003). The non-miliolids also have been reported from wide environmental ranges on coral reefs. For example, *E. repandus* occurs not only in semi-protected and offshore lagoons in Bermuda but also in the inner and outer fore-reefs
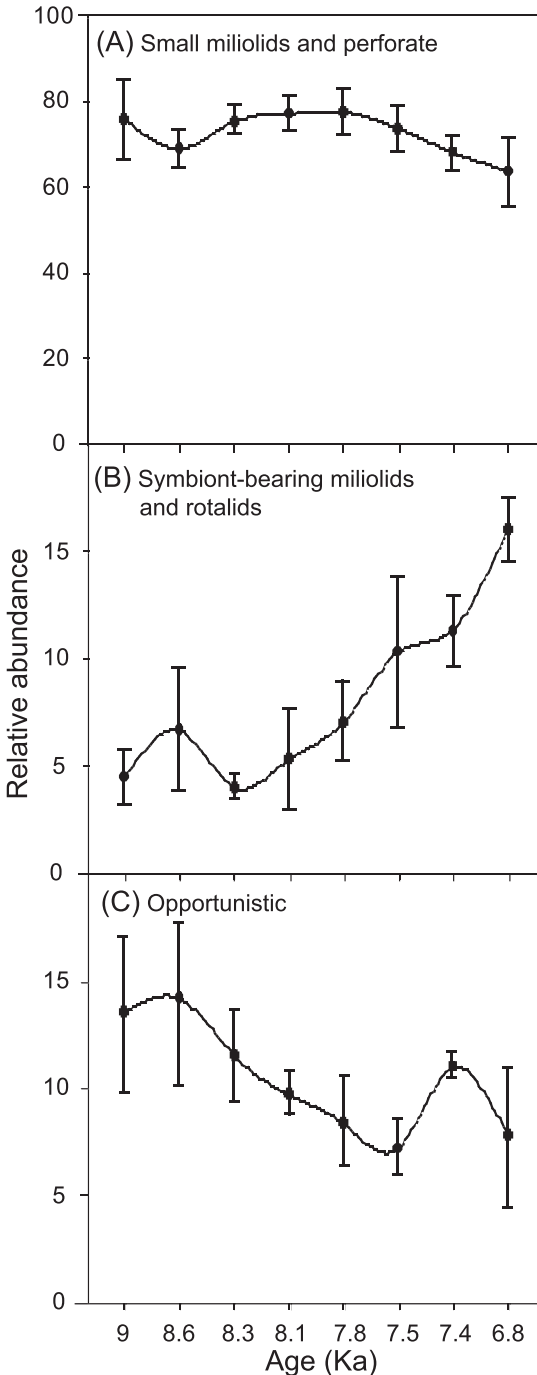
FIGURE 5. Plots of relative abundance of three prominent foraminiferal functional groups from the Holocene Bonah River section, Huon Peninsula, PNG. A, Small miliolids and perforates remained relatively constant. B, Symbiont-bearing miliolids and rotalids steadily increased throughout the section. C, Opportunistic species steadily decreased throughout the section. A slight shift in all functional groups occurred after the volcanic eruption (between 9 and 8.6 Ka). The y-axis refers to the relative abundance of individuals contributing to one of the three

←

major functional groups (means ± standard error). Note the y-axis scale differences among the three functional groups.
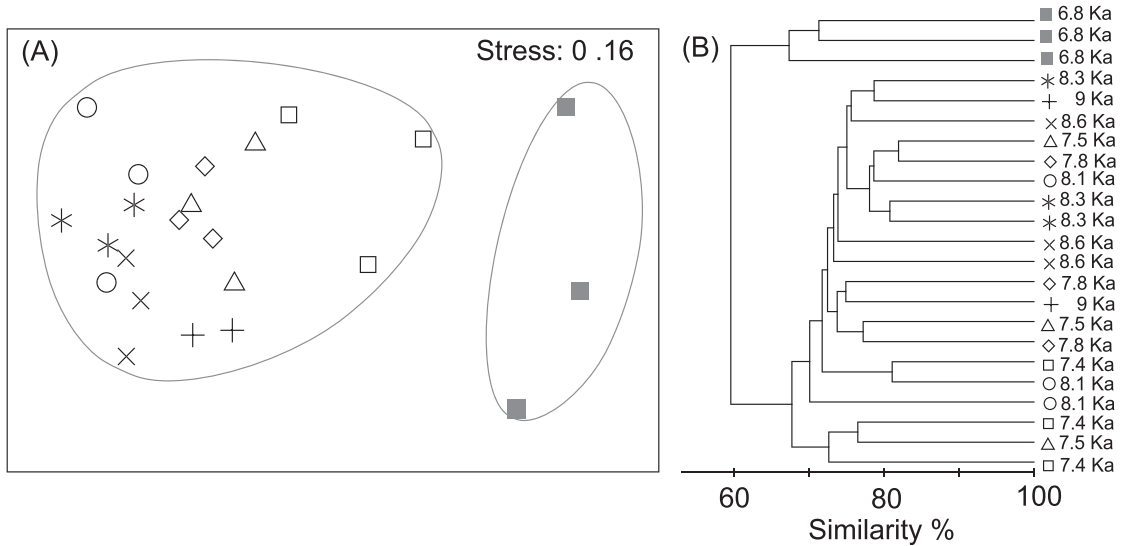
FIGURE 6. A, Nonmetric multidimensional scaling (NMDS) ordination of Holocene foraminiferal assemblages based on the Bray-Curtis similarities from the eight time periods sampled along the sea cliffs at Bonah River, PNG. Symbols indicate replicate samples from each of the eight vertically stacked 25-m-long horizontal transects taken along the seacliff face. The two ovals surrounding the points in the NMDS plot represent the 60% similarity grouping. B, The group average cluster analysis shows the division between communities sampled from the seven older transects and those sampled from the youngest (6.8 Ka) temporal horizon. Persistent overlap in community similarity characterized the foraminiferal communities sampled from the seven older time periods.

(5–60 m depth) of Florida-Bahamas, Venezuela, and Barbuda (Javaux 1999). *Rosalina globularis* is characteristic of Bermuda mangrove and lagoon assemblages, where it displays large morphological variability, and is reported in nearshore waters and lagoons of the Florida-Bahamas and on the Belize Shelf (Javaux 1999). In summary, the highly abundant heterotrophic species found at Bonah River in the Huon Peninsula have a wide geographical range and are distributed across a variety of reef types.

Foraminifera are often used to detect environmental change in both modern (Alve 2003; Schueth and Frank 2008; Uthicke and Nobes 2008) and ancient (Duchemin et al. 2005;

TABLE 2. Results of the Mantel test between matrices represented by similarity in foraminiferal community composition and time separating communities (centuries to millennia) from the Bonah River section at the Huon Peninsula, PNG.

	df	Sum sq.	Mean sq.	F	p	Rho
Model	1	4281.90	4281.90	129.73	0.0001	0.387
Error	251	8284.61	33.01			
Total	253	12,566.50				

Dominici et al. 2008; Reolid et al. 2008) settings. Reef foraminifera from Madang Lagoon, Papua New Guinea, showed limited faunal mixing among habitats, so death (and fossil) assemblages are reliable paleoecological indicators of coral reef habitats (Langer and Lipps 2003). The temporal distribution of the foraminiferal assemblages from Bonah River suggests that the reef environment maintained ecologically similar conditions throughout most of the Holocene sea-level rise. However, the changes in functional groups with an increase in symbiont-bearing taxa (Fig. 5) may have resulted from a decrease in water depth as accommodation space lessened during the later phases of Holocene sea-level stabilization. Despite the broad environmental tolerances of the most abundant foraminiferal species at Bonah River, three other taxa that show strong environmental preferences provide additional clues as to the changes in foraminiferal communities through time. Species belonging to *Elphidium* are typical of shallow water habitats, usually associated with areas of high light in less than 10 m water depth, and so are commonly used as sea-level indicators (Sen Gupta 2003a). *Elphidium* spp. occurred regularly, but in low
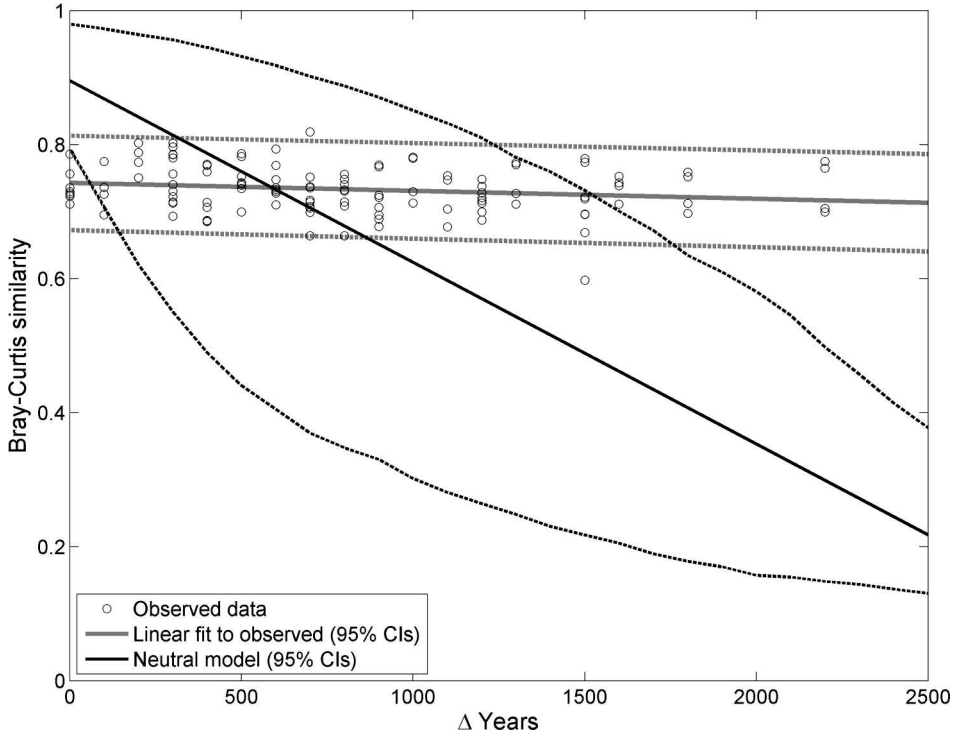
FIGURE 7. Plot of Bray-Curtis similarity index versus time separating samples for observed foraminiferal communities, and those derived from the neutral model, throughout the 2200-year interval represented in the Bonah River section of the Huon Peninsula, PNG. Open circles represent all pairwise similarity comparisons within the observed community. Gray lines represent best-fit linear regression to these similarities based on time elapsed (mean, solid lines; 95% confidence intervals, dotted lines). The gradient of this linear regression is the CII of the observed communities. The black lines represent the equivalent neutral model (mean and 95% confidence intervals). Plot is for a total community size of $J = 50,000$ individuals.

abundances throughout the older time intervals, and the genus became a major contributor to the community composition only in the younger time periods (7.4 Ka and 6.8 Ka). Another genus that exhibits a strong depth zonation is *Amphistegina*, which is associated with water depths of less than 10 m or exceptionally transparent water below 30 m (Hallock 2003). *Amphistegina* only started to appear in the younger reefs at the same time *Elphidium* became prevalent. Lastly, one of the few infaunal foraminiferal species found in this study, *Gyroidina neosoldanii*, began to increase in abundance only in the younger transects. Jorissen (2003) interpreted the transition from abundance of epifaunal to infaunal foraminiferal species as shifts in microhabitat preference as space or nutrients become limiting or predation increases. Such increases of infaunal foraminifera at the top of the Bonah River section coincide with other changes in the benthic

foraminiferal communities in the waning phases of reef growth, which we discuss next.

Community Change through Time

Our results record a foraminiferal community that showed only incremental changes in community composition through time (Table 2), but no changes in species diversity or evenness (Table 1, Fig. 2) or species rank abundance (Fig. 3). Persistence in diversity is a feature of both terrestrial and marine ecosystems over geological time frames (Brett et al. 1995, 1996; DiMichele et al. 2004; Ivany 1996; Morris et al. 1995). However, Patzkowsky and Holland (2007) described Ordovician macro-invertebrate communities from tropical marine ecosystems open to invasion where diversity increased for up to a million years. Pleistocene coral reefs both from transgressive sequences built during sea-level
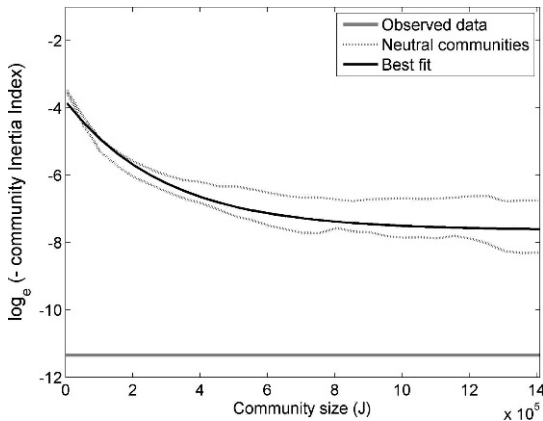
FIGURE 8. Community inertia index (CII) from observed and neutral communities of the Bonah River section of the Huon Peninsula, PNG, as a function of metacommunity size. The CII values are the gradient of a linear fit to the temporal change in the Bray-Curtis similarity of neutral metacommunities. The y-axis is the log-transformed magnitude of the resultant negative CII value; the larger the negative value, the greater community inertia. The x-axis is the theoretical metacommunity size from which the observed samples were collected; note the scale is multiplied by 10^5. The gray line represents the CII of the observed foraminiferal community. The dotted lines indicate the 68% confidence intervals of the CII for equivalent neutral communities of increasing size (i.e., within one standard deviation of the mean). Note that neutral communities change much faster than the observed foraminiferal communities. Furthermore, the best-fit exponential trend to the neutral results (solid line) indicates that neutral communities will have lower inertia for any reasonable metacommunity size.

rise (Pandolfi 1996) and from regressive sequences built during sea-level falls (Tager et al. 2010) show consistent levels of diversity through time. Our study shows that these long-term patterns in species diversity can persist in the presence of significant episodes of disturbance.

Only foraminiferal communities from the latest time period were substantially distinct from those of the seven earlier time periods. Surprisingly, community composition was relatively invariant before and after the eruption-induced mass mortality event early in the sequence. In the centuries following the volcanic eruption, the foraminiferal assemblages remained consistently above 60% similar for 1500 years (9 Ka–7.5 Ka). During this time sea level rose and the reef "kept up" by growing on average 1 m per 300 years. After this period of consistent reef growth, reef accretion slowed dramatically to 1 m in

600 years between the youngest two transects. We view this decline in reef growth as a response to the reduction of the accommodation space (water depth between sea level and reef accretionary surface), typical as sea-level rise slows and reefs approach maximum sea level (Chappell and Polach 1976, 1991; Samankassou 1997; Braithwaite et al. 2000). Significant changes in the foraminiferal assemblages coincide with this environmental shift, for example, a threefold increase of *Eponides repandrus* in the youngest transect (Fig. 4). In terms of community response to disturbance, a striking pattern emerges: there was a greater response of foraminiferal communities to the "press" (Connell 1997) chronic long-term disturbance of sustained sea-level change than there was to the "pulse" (Connell 1997) acute, short-term disturbance of instantaneous mass mortality due to the volcanic eruption.

Ecological Drivers

Despite the differences in foraminiferal community composition in the younger part of the reef sequence, overall our observed foraminiferal communities were far less variable than communities predicted from neutral theory (Fig. 7). For a large part of the Bonah River section, the foraminiferal communities showed no decay of similarity through time (i.e., high inertia), remaining constant until changing environmental conditions led to the reduction of accommodation space in the later phases of transgressive reef growth. However, even with the corresponding increase in symbiont-bearing species, community similarity showed little change (ranging from ~0.60 to 0.82) throughout the temporal sequence (Fig. 7). In contrast, foraminiferal communities derived from neutral theory expectations displayed a continuous and relatively rapid drift toward communities that were greatly dissimilar from the initial communities (Fig. 7). These results occurred regardless of the size of the foraminiferal metacommunity—projecting forward from our simulations, a neutral metacommunity that exhibited the low CII of the observed foraminiferal data set would have to be almost infinitely large (Fig. 8). They were also robust

to our assumptions about the degree of inter-connectedness (dispersal) between foraminiferal communities. Our results show neutral CII values under assumptions of panmixia—but the presence of dispersal limitation ($m < 1$) would increase the discrepancy between neutral and observed community inertia even further. From this we conclude that the ecological dynamics of the observed foraminiferal community over the time scale of the study is distinctly non-neutral, even during both ''press'' and ''pulse'' disturbance events occurring at large spatial scales. Hubbell (1997) argued that the ''law of large numbers'' will ensure that the common species remain common in coral reef communities through time (and may result in similar species rank distributions through time), but the inertia observed in the Holocene foraminiferal community is too great for a neutral community to emulate, no matter what its size.

Expansion of our study to include more sites and environments along the Huon Peninsula will provide us an opportunity to test the relative importance of disturbance regime and environmental variation on the patterns of community inertia and persistence in species diversity found at the Bonah River site. For example, McGill et al. (2005) showed, using decay curves for CII in Quaternary mammals, that community similarity increased with higher taxonomic levels and greater geographic variation. The lower values of CII for our Holocene foraminifera (Pearson's $r = 0.7$) than for mammal communities of North America (Pearson's $r = 0.9$) might increase if examined over greater spatial and temporal scales (Pandolfi 2002).

If communities are non-neutral, then what processes might be driving this community inertia? We are aware that we have documented ecological *patterns* through time, and that determining ecological mechanisms thus falls beyond the scope of our study. However, one hypothesis for long-term patterns in community composition that show no or only incremental change in species abundances might be incumbent species advantages over both invasive species (Valentine 1980, 1990; Van Valen 1985; Rosenzweig and McCord 1991; Jablonski and Sepkoski 1996) and the

subsequent proliferation of less common or rare species (Case 1991; Pimm 1991; Massot et al. 1994). Non-neutral dynamics may have resulted from ecological incumbency of well-established foraminiferal species at the Bonah River site, at least in the post-mortality event assemblages. If so, then history matters, and incumbent species within sites may be difficult to dislodge under natural conditions of reef growth, with an advantage due either to having greater familiarity with the local environment or to being competitively dominant (Massot et al. 1994).

Incumbency in the foraminifera over the disturbance interval must have been due, at least in part, to their relative ability to recolonize from adjacent environmental and geographic settings, given that similar species would have maintained populations outside of the affected areas. However, processes other than ecological incumbency might also have contributed to the patterns we have seen. The large-scale mass mortality caused by the volcanic event would have eliminated all incumbents over a reasonably large spatial scale, and, consequently, most advantages of incumbency. Nevertheless, the community returned to a very similar state following this event, suggesting other deterministic processes besides incumbency. A number of stabilizing processes, such as resource partitioning and the ''storage effect,'' have been suggested for the maintenance of species diversity in communities (reviewed in Chesson 2000), and on coral reefs the interaction between disturbance (Karlson and Hurd 1993) and niche partitioning (Knowlton and Jackson 1994) over long time frames may help to ensure persistence in both community composition and diversity.

Regardless of the specific mechanisms involved, our results support the view that Holocene foraminiferal communities maintained similar species assemblages over extensive periods of time. As such it provides managers with a history of the natural range in variation of PNG reef foraminiferal communities in the absence of modern anthropogenic stressors. It is now well known that degradation on coral reefs is occurring at a very rapid rate, especially among the reef-builders, the scleractinian corals (Pandolfi et al. 2003). However, knowledge of

the historical variability in reef constituents provides managers with a way of knowing what was natural in the past, which provides context for setting appropriate management goals. The success of management actions vis-à-vis these goals is enhanced by comparison with past ecosystem states. Thus, in attempting to conserve the biological diversity of living reefs, study of the past history of Quaternary reefs should provide context for management and restoration of degraded species assemblages.

Acknowledgments

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