

## **A HABITAT-BASED PERSPECTIVE OF MARINE BIOGEOGRAPHY IN PASSIVE AND CONVERGENT TECTONIC SETTINGS**

Bjørn-Gustaf J. Brooks and Cinzia Cervato

### **ABSTRACT**

The dominant biodiversity paradigm in the Earth sciences has been that abiotic forces such as orbital variations, bolide impacts, and volcanism, among others, are the primary drivers of extinction and biodiversification. By describing several instances when increased tectonism and biodiversity hotspots coincided, a recent study of fossil foraminifera indicated that over the past 50 million years (m.y.) the predominant driver of biodiversity has been plate tectonics. We test whether this hypothesis holds true for assemblages of marine macrofossils from temperate latitudes using one of the most comprehensive data sets of its kind, the Paleobiology Database. Our multivariate statistical approach provides a base for examining the historical biogeography of marine macrofossils and for investigating ecosystem interactions on various scales. We began by examining the biogeographical patterns across 40 phylogenetic classes of marine animal macrofossils spanning the most recent 57 m.y. in both passive and convergent tectonic settings using area-standardized alpha and beta diversity components at the species and genus level. When the diversity components of average grid cells were compared between regions, the highest alpha diversities occurred in the passive tectonic setting of the eastern United States. We tested whether this could be due to biased coverage of North American fossils by rarefying and recomputing our diversities. Although the subsequent alpha diversities were more homogeneous, eastern North America was still the most diverse.

To explore the connection between this observation and ecological niche theory, we simulated paleo-habitats for each grid cell using a multivariate *k*-means clustering of the lithological annotations of occurrences within grid cell assemblages. Across 83,000 occurrences, the number of simulated habitat types within a grid cell was significantly correlated to the alpha diversity of that grid cell (species-level  $r = 0.763$ , genus-level  $r = 0.857$ ). Further tests using rarefied subsets of occurrences did not strongly impact this correlation (species-level  $r = 0.679$ , genus-level  $r = 0.762$ ). Our results, which apply to Cenozoic marine macrofossils, imply that a more robust predictor of alpha diversity across both passive and convergent tectonic settings is the diversity of paleo-habitat types. This investigation provides statistical evidence that simulated habitat types from lithologies can be used as a rudimentary analogue for ecosystem complexity, and that the abundance of habitats scales linearly with the alpha diversity of fossil assemblages.

Bjørn-Gustaf J. Brooks. Department of Geological and Atmospheric Sciences, Iowa State University, 253 Science I, Ames, Iowa 50011, USA.

Center for Climatic Research, University of Wisconsin-Madison, 1225 West Dayton St. Madison, WI 53704, USA. bjorn@climatemodeling.org

Cinzia Cervato. Department of Geological and Atmospheric Sciences, Iowa State University, 253 Science I, Ames, Iowa 50011, USA. cinzia@iastate.edu

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## INTRODUCTION

The controls of biodiversity today and throughout Earth history are an important theme to much of biology and geology. A recent study of the biodiversity of marine microorganisms spanning the past 50 m.y. (million years) has revisited an important topic concerning the influence of plate tectonics on biodiversity (Renema et al. 2008). By examining the genus-level alpha diversity component of benthic foraminifera throughout tropical to temperate portions of Europe, Asia, and Australia, Renema et al. (2008) measured the greatest alpha diversities during epochs of convergent tectonic activity. A related study of this topic that also covered the Indo-Australian Archipelago (IAA) was published more than two decades earlier by Whitmore (1982) who similarly showed that the essential component that determines the exceptional present day biodiversity there was convergent tectonics between Asia and Australia. Although the confluence of species gave the region an anomalously high biodiversity, earlier researchers were surprised to find that most species generally inhabited their original continent, with ranges that mirrored the plate boundary. Wallace (1860), too, was intrigued that species obeyed such a sharp zoogeographic boundary (Wallace's Line) and even alluded to a possible continental plate explanation for the phenomenon.

In the rock record contribution from other factors such as species competition and moderate disturbance have no doubt been influential, but their observation has been difficult. Deterministic events such as bolide impacts (Schulte et al. 2010) or extensive volcanism (Renne et al. 1995; Self et al. 2006) are perennial favorites in geology that are invoked as explanations for biodiversity crashes and their subsequent biodiversification events. The strength of causality arguments for such coincidental events are limited because the Earth has many times been subjected to asteroid impacts (among other major calamities), and they are seldom asso-

ciated with major extinctions. On the other hand, factors important to the study of present day biodiversity including coexistence, immigration, and resource gradients have received much less coverage by Earth scientists, in part because these factors are more difficult to quantify through fossil evidence. This situation is changing today, because fossil data sets now (e.g., Alroy et al. 2008) provide extensive information sufficient to test for other drivers of biodiversity and biogeography.

The focus of this paper is to simulate marine ecosystem habitat types in order to investigate patterns in biogeography in passive and convergent tectonic settings. To do so several diversity measures are compared at both the genus and species level (using complete and rarefied subsamples) between surface area standardized grid cell assemblages from eastern North America, Europe, and Japan. Our collection of assemblages spans the most recent 57 m.y., a period over which the continents have occupied roughly the same present day latitudes, and the fossil record is particularly well preserved. Ecosystem factors such as water depth were parameterized from the lithologic annotations of each fossil occurrence, and a *k*-means algorithm was used to designate habitat types and to compare patch structure between grid cells. We further discuss these relationships with regard to sampling bias, latitudinal gradients in species diversity, and sampling resolution, all of which set important bounds on the inferential scope of our results.

## METHODS

In this section we describe the data used and our methods for determining diversities. We also describe our methods for additional tests using subsampling (rarefaction) and simulated habitat types. Extant communities can have spatially open configurations in which the inhabitants of one community can extend into neighboring communi-

ties (Whittaker 1972). To avoid confounding the analysis with such extant communities and to examine long-term relationships between biodiversity and tectonism, diversity measures are expressed per grid cell assemblage of fossils. We define an assemblage grid cell as the collection of marine fossil occurrences per 10,000 km. We calculated this by first computing the diversity measures for each grid cell (1° longitude x 1° latitude) and then scaling to a standard grid cell surface area assuming a spherical Earth. Each non-empty grid cell contained one or more co-occurring fossil observations, which contributed to its alpha and beta diversity. As in extant ecosystems, grid cells may consist of multiple habitat types, within which many of the activities of these marine populations occurred. In the absence of ecological observations, the lithological annotations of each fossil occurrence were used to simulate and assign each to a habitat type using a multivariate statistical clustering method. Source pool diversity and connectivity were also calculated for the neighborhood of each grid cell. Statistical properties of these indexes were analyzed regionally and through time.

### Paleobiology Database

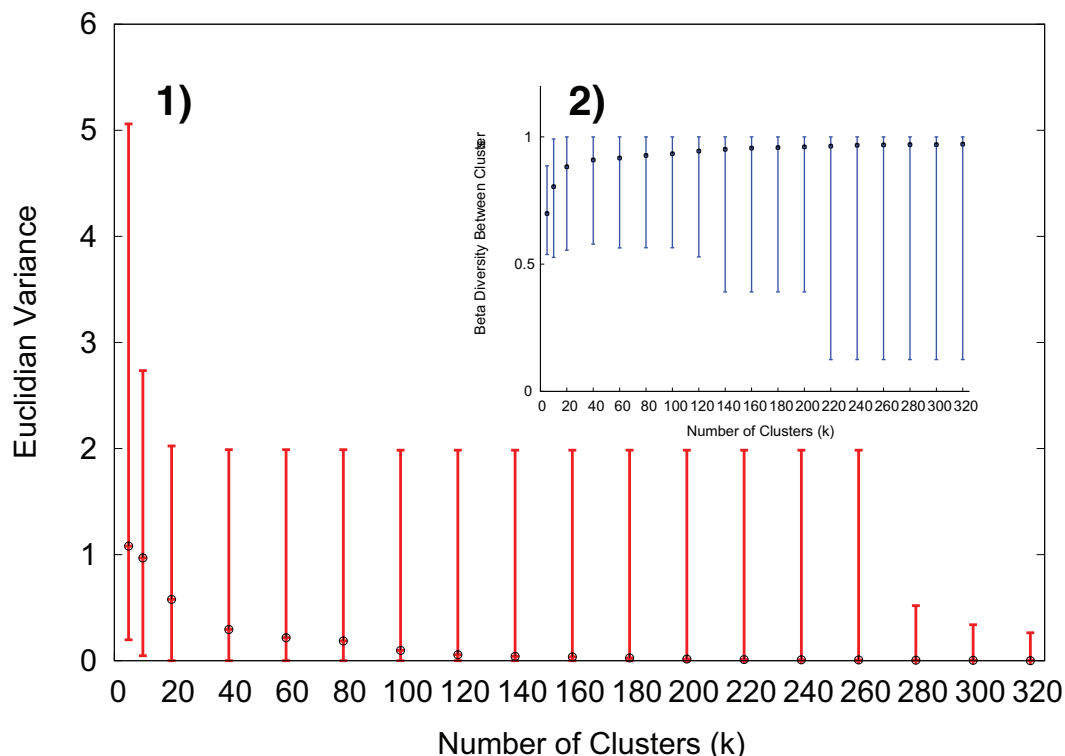
Our data were derived from the Paleobiology Database (PD 2008), one of the most extensively annotated compilations of fossil occurrences to

date (Alroy et al. 2008). We focused our analysis on the most recent 57 m.y. of these data, which contain many of the best preserved and most detailed specimens of the fossil record. These 83,213 occurrences represent 8,821 published articles and include 25,595 species (5,773 genera) and 40 phylogenetic classes of marine fossil organisms. Of the 77,820 phylogenetically annotated occurrences (23,330 species), 62,689 (81%) occurrences or 17,446 (75%) of the species belong to the phylogenetic classes Bivalvia or Gastropoda (Table 1) indicating that mollusks are particularly well represented in the PD (Crame 2009).

Each occurrence downloaded from the PD is annotated with an environment of deposition and several fields describing lithology. We converted these observations from categories to numerical values using the PD's data entry criteria (PD 2008). For example, the depositional environment "fore-shore" in the PD is reserved for occurrences with reported lithologies that are indicative of the intertidal zone between high and low tide. The mean of that range (zero) was taken to be the water depth for such an observation, as it was either submerged or emergent depending on the tide. Thus, for each of the 421 environmental and lithological combinations in our downloaded data, we have designated values for water depth and the percentage of sand, silt, clay, and lime mud (see Appendix Table 1). The subsequent scalar values for depth,

**TABLE 1.** Species level data composition. Species abundances of select phylogenetic classes, total species, and the number of habitat types within each sub-epoch are listed. Epoch and sub-epoch ages correspond to the ages of their base. 1 Species level data composition. Species abundances of select phylogenetic classes, total species, and the number of habitat types within each sub-epoch are listed. Epoch and sub-epoch ages correspond to the ages of their base.

Interval	Time (Ma)	Duration (m.y.)	Bivalve Species	Gastropod Species	Total Species	Habitat Types
Holocene	0.00	0.00	241	279	651	15
Pleistocene	2.6	2.59	1188	1835	4017	29
Pliocene	5.3	2.7	1324	1891	4644	28
late Miocene	11.6	6.3	1258	1422	3568	33
middle Miocene	16.0	4.4	1374	1286	4081	33
early Miocene	23.0	7.0	1439	1813	4441	32
late Oligocene	28.4	5.4	597	412	1518	30
early Oligocene	33.9	5.5	721	699	1792	25
late Eocene	40.4	6.5	926	1287	3419	34
middle Eocene	48.6	8.2	954	1020	3002	32
early Eocene	55.8	7.2	329	475	1377	19



**FIGURE 1.** Cluster selection and variance across clusters. These show that the difference between clusters and the total variance of each cluster declines with increasing numbers of clusters, but the gain is negligible for values greater than  $k = 40$ . 1.1) Scree plot of the Euclidean variance across cluster centroids. The red whiskers show that the total variance diminishes with increasing numbers of clusters, while the mean variance among the cluster centroids, indicated by the black dot, approaches zero. 1.2) Blue whiskers and black dots indicate that as the number of clusters increases, the mean beta diversity (difference) and its variance increase—clusters become more specific, and thus more different.

sand, silt, clay, and lime mud were used as environmental characteristics to define the hyperspace volume for each habitat type within its landscape using cluster analysis.

#### Habitat Type Determination

In order to simplify exposition and computations of the data, a multivariate statistical cluster analysis technique, based on the  $k$ -means procedure of Hartigan (1975), was employed to identify unique habitat types, following the method used for ecoregionalization by Hargrove and Hoffman (2004). An improved version of a parallel clustering algorithm, developed by Hoffman and Hargrove (1999), was run on a high performance cluster computer. The clustering procedure consists of two parts: initial centroid or seed determination and iterative clustering of observations (fossil occurrences) until convergence is reached. Initial centroids (seeds), one for each of the  $k$  clusters, were

selected at random from the fossil occurrence data. In the iterative clustering algorithm, fossil occurrence records are assigned to the nearest centroid, by Euclidean distance, in the  $m$ -dimensional phase space formed from the  $m$  environmental characteristics included in the analysis. Once all records are assigned to a centroid, the centroid locations in this phase space are recomputed as the mean of the observations assigned to that centroid. This process repeats until only a small number of observations are assigned to a different cluster between iterations. For this study, the convergence criteria was 0.5% of the  $n$  fossil occurrence records.

Since the number of clusters,  $k$ , is chosen a priori by the user, a series of clustering trials, with  $k = 5, 10, 20, 40, 60, \dots, 320$ , were performed to determine a reasonable level of division for the data. Figure 1 shows a scree plot of the mean Euclidean variance for clusters at different levels of division.

**TABLE 2.** *k*-means habitat type assignment. Given the PD's lithological data we accordingly assigned each observation to one of 40 habitat types using *k*-means clustering (see also Appendix). "int." indicates interdistributary and "sst" indicates sandstone.

Observation	Depositional Environment	Depth (m)	Primary & Secondary Lithology	Sand (%)	Silt (%)	Clay (%)	Lime Mud (%)	Hab. Assgn.
<i>C. pygmaea</i>	offshore	200	siltstone only	0	0	83.3	16.7	27
<i>C. pygmaea</i>	offshore	200	shale only	0	0	33.0	67.0	38
<i>E. ovatus</i>	shoreface	15	sandstone only	100	0	0.0	0.0	16
<i>G. vulcanica</i>	int. bay	0	mudstone & sst	28	8	35.6	35.6	35

Around  $k = 40$  this mean variance is reasonably small while the number of clusters is not too large to analyze. Therefore, the results presented here will be primarily for  $k = 40$ . Because clustering results can also be somewhat sensitive to the selection of initial centroids (seeds), a number of clustering trials were performed with different random seeds. Statistical correlations were consistent across the trials, so the results presented are not sensitive to the starting seeds. Table 2 shows example results of the clustering procedure.

### Alpha and Beta Diversity

We used two primary measures of biodiversity: alpha diversity, the latitudinally scaled diversity of fossil species (or genera) within one grid cell, and Whittaker's beta diversity, the species or generic difference between two grid cells (Whittaker 1972). Beta diversity is calculated as  $D_c/D_b - 1$ , where  $D_c$  is the total diversity of species (or genera) in the composite of two grid cells, and  $D_b$  is the mean diversity of species (or genera) from both grid cells. Empty grid cells, those without fossil occurrences, were excluded. For any grid cell assemblage,  $A_i$ , that touched only one occupied neighboring grid cell,  $N = 1$ , the calculation of beta diversity was exactly as described above. For any  $A_i$  where  $2 \leq N \leq 8$ , beta diversity was calculated as the mean of all betas in the neighborhood (see Appendix Table 3). To complete the neighborhood for grid cells located at geographical edges (e.g., longitude  $179^\circ$  W to  $180^\circ$  W), we wrapped these neighborhoods to include grid cells at the opposite geographic extreme (e.g., longitude  $179^\circ$  E to  $180^\circ$  E). No occupied grid cells in our data set appeared at latitudes above  $89^\circ$  north or south, therefore it was not necessary to wrap over the poles.

### Source Pool Diversity and Connectivity

For the neighborhood of each grid cell we measured two additional indexes that describe the

spatial continuity of these fossil data: source pool diversity and connectivity. Source pool diversity is equivalent to the total alpha diversity of the neighborhood excluding the grid cell of interest. Connectivity is the proportion of occupied adjacent grid cells. We express this as a ratio between 0 and 1, with 1 being a neighborhood in which each of the 8 neighboring grid cells is occupied by at least one fossil observation.

### Subsampling Routine (rarefaction)

To test whether or not the correlations between diversity measures and simulated paleo-ecosystem factors could be the result of biased sampling intensity, assuming that the abundance of occurrences reflects sampling intensity, we computed diversity  $D$  from the complete list of fossil occurrences  $L_i$ , and from the mean of 100 rarefied lists  $L_i$ . For rarefied lists we randomly selected 100 fossil occurrences from each grid cell's fossil occurrence list using a uniformly distributed pseudo-random number generator (Park and Miller 1988). Each rarefied occurrence list represents a random subsample of its original list. Thus the rarefied diversity  $D_i$  of a grid cell assemblage  $A_i$  is computed as the sum of unique genus ( $G$ , or species names  $S$ ) drawn from  $L_i$ , where  $L_i$  is a random subsample of  $L_i$ . In computing  $L_i$  for each region in each sub-epoch in Table 3 we instead used occurrence lists of length 15 rather than 100 in order to consistently include Japan, which generally had occurrence lists shorter than 100.

## RESULTS

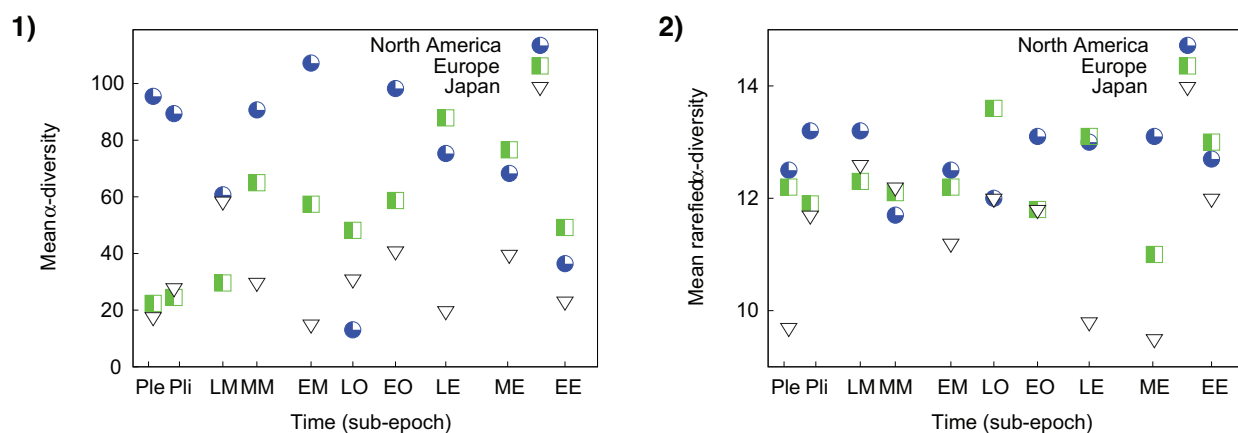
Biodiversity measures reported in the main paper are given at the species level, which is where the effects of ecosystem factors would be most apparent. Genus level diversity measures are very comparable, generally with correlation coefficients similar to within 0.1 or less. Complete tables of genus level diversity measures appear in Appendix Table 6. A time series of diversity mea-

**TABLE 3.** Local species diversity by region. Mean abundances per grid cell (10,000 km) for alpha, beta, habitat type, source pool diversity, and connectivity are given for each sampling interval. Values in parentheses indicate rarefied alpha diversity, which is not given for the Holocene due to sparseness of the data. Asterisks indicate peak values, except for early Eocene European beta diversity, which was a local peak. Europe and Japan represent convergent tectonic settings, and eastern North America represents passive.

Interval	Region	Alpha-Div.	Beta-Div.	Habitat Types	Source Pool Div.	Connectivity
Holocene	E. N.Am.	44.3	0.00	2.2	1	0.00
	Europe	61.6	0.00	6.3	1.2	0.00
	Japan	4.5	0.67	1.3	1.9	0.08
Pleistocene	E. N.Am.	95.5 (12.5)	0.87	5	281.6	0.40
	Europe	22.4 (12.2)	0.52	2.3	32.3	0.16
	Japan	17.7 (9.7)	0.75	2.2	18.4	0.14
Pliocene	E. N.Am.	89.4 (13.2)	0.82	4.5	268.5	0.35
	Europe	24.5 (11.9)	0.74	3.1	33.9	0.14
	Japan	27.9 (11.7)	0.73	3.3	28.4	0.12
Late Miocene	E. N.Am.	60.7 (13.2)	0.90	5.1	104.4	0.21
	Europe	29.6 (12.3)	0.75	2.8	57.9	0.19
	Japan	58.5 (12.6)	0.73	4.7	114.8	0.21
Middle Miocene	E. N.Am.	90.7 (11.7)	0.57	4.7	122.3	0.11
	Europe	65.0 (12.1)	0.69	4.5	141.9	0.23
	Japan	29.8 (12.2)	0.86	2.8	47.3	0.20
Early Miocene	E. N.Am.	107.2 (12.5)	0.93	5.8	207.4	0.30
	Europe	57.4 (12.2)	0.49	3.7	37.7	0.10
	Japan	15.1 (11.2)	0.60	2.7	12.8	0.11
Late Oligocene	E. N.Am.	13.1 (12.0)	0.22	2.9	1.9	0.03
	Europe	48.2 (13.6)	0.26	5.1	9.7	0.04
	Japan	31.0 (12.0)	0.65	4.9	27.1	0.12
Early Oligocene	E. N.Am.	98.3 (13.1)	0.77	4.7	192.4	0.30
	Europe	58.7 (11.8)	0.47	4	5	0.09
	Japan	40.9 (11.8)	0.13	2.5	9.9	0.02
Late Eocene	E. N.Am.	75.3 (13.0)	0.83	4.7	170.5	0.21
	Europe	87.9 (13.1)	0.57	7	123	0.12
	Japan	19.8 (9.8)	0.57	3.4	23.1	0.10
Middle Eocene	E. N.Am.	68.3 (13.1)	0.88	5.2	110.7	0.23
	Europe	76.6 (11.0)	0.58	4.5	177	0.16
	Japan	39.7 (9.5)	0.69	4	52	0.22
Early Eocene	E. N.Am.	36.4 (12.7)	0.82	6.6	53	0.22
	Europe	49.2 (13.0)	0.68	4	127.9	0.26
	Japan	23.2 (12.0)	0.00	1.1	1.1	0.00

tures that compare passive and convergent tectonic settings is presented in Table 3 and Figure 2, with rarefied diversity shown in parentheses. Table 3 shows an alpha diversity peak in Europe in the Eocene, during a protracted period of collision

between Africa and Europe that resulted in the orogeny of the Pyrenees (Burbank et al. 1992; Vergés et al. 2002). Japan, which experienced tectonism continuously throughout the past 50 m.y. (Hall 2002), and Table 3 shows an alpha diver-



**FIGURE 2.** Mean alpha diversity for area-standardized grid cells by region from the Pleistocene through Early Eocene (57Ma-0Ma). 2.1) Alpha diversity using the complete occurrence lists. 2.2) Alpha diversity using rarefied occurrence lists. These show that North America is the most diverse through most subepochs even using rarefied diversities, and that there is a general increasing trend in North American un-rarefied diversity toward the present (left of plot), as opposed to a decreasing diversity trend in Europe. These trends however, disappear when rarefied plots are compared.

sity peak during the late Miocene. It should be noted that data from other tectonically active regions, such as the Indo-Australian Archipelago, are not reported in Table 3 because they were not well represented in this data set.

Consistently the most diverse region in complete and rarefied alpha diversity was eastern North America where marine fauna existed along a passive continental margin (Table 3 and Figure 3). The average alpha diversity per grid cell in eastern North America computed from complete occurrence lists was 87.8, ahead of Europe ( $\alpha = 56.1$ ), and Japan ( $\alpha = 31.5$ ). Although rarefied alpha diversity numbers between the three regions were more homogeneous, ranging from 9.5 to 13.6, eastern North America was still the most diverse overall and consistently the most diverse in six of ten sub-epoch. The beta diversity components indicate that the average eastern North American grid cell ( $\beta = 0.81$ ) was more different from its neighbors, than was the case in Europe ( $\beta = 0.62$ ) or Japan ( $\beta = 0.67$ ).

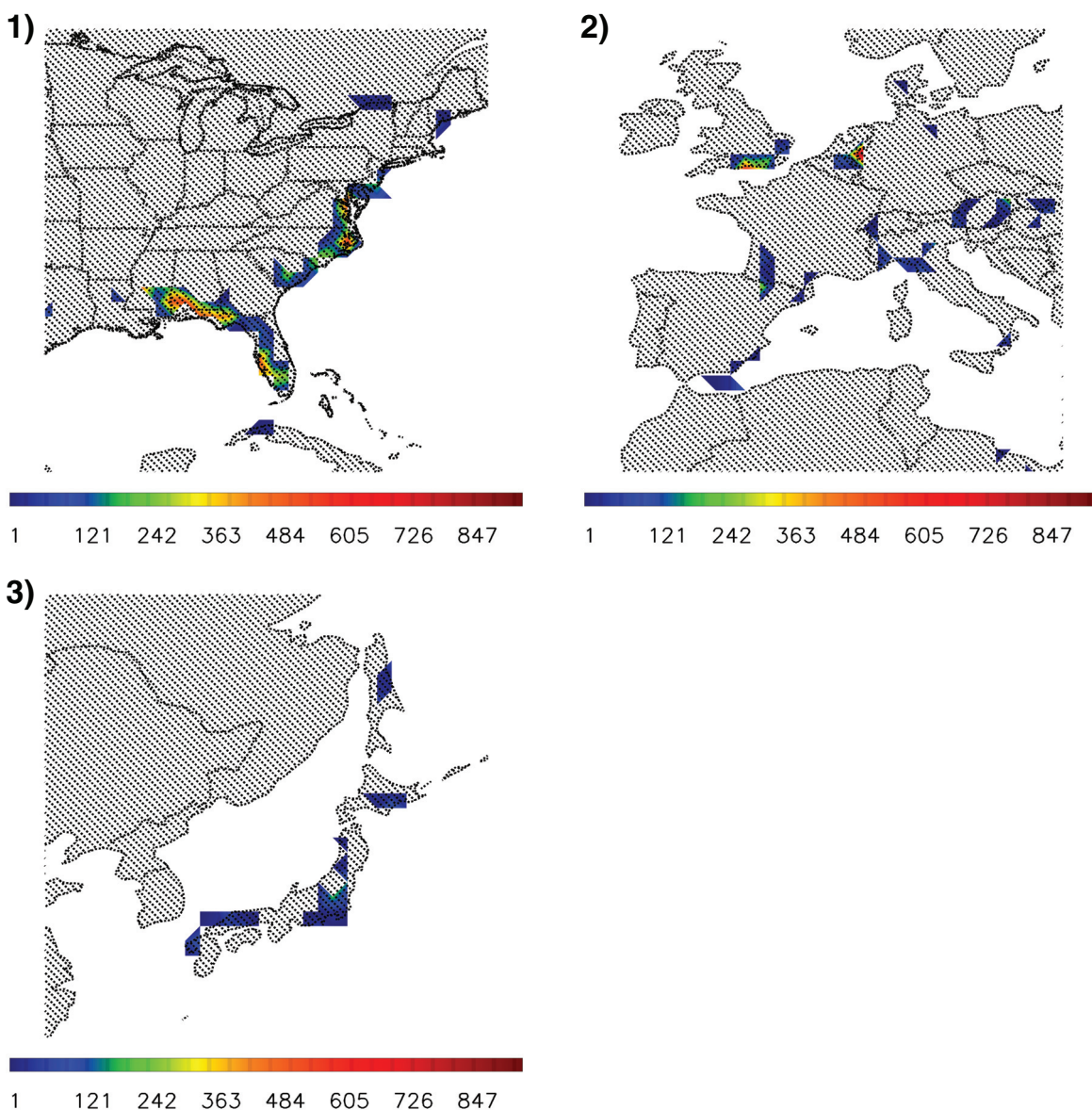
When all 1,565 globally distributed grid cells were considered, correlation tests between diversity measures indicated that the two most related factors were the diversity of  $k$ -means habitat types and alpha diversity (at species level:  $r = 0.763$ , at genus level:  $r = 0.857$ , see Figure 4 and Table 4). Rarefied subsetting slightly decreased these correlations, but generally by less than 0.1 (at species level:  $r = 0.679$ , at genus level:  $r = 0.762$ , Appendix Table 6). Because the diversity of habitat types rep-

resents a clustering of multiple parameters, correlations to the constituent parameters were also tested. Insignificant correlations occurred between alpha diversity and all such parameters including water depth, percent sand, silt, clay, and lime mud (see Table 4). The beta diversity component showed no correlation to other parameters, except a possibly significant correlation to connectivity ( $r = 0.632$ ), which represents the spatial (not ecological) connectivity of grid cells.

The robustness of the habitat type–alpha diversity correlation was tested against two null models. The first null model was used to decipher our method of clustering from random chance by assuming that habitat type correlations could be the result of analytical chance introduced by our clustering algorithm. We performed 100 random seed cluster trials, each of which started with a different collection of  $k$  seed centroids. The data were then analyzed as described above and correlated. The species level correlations from the 100 random trials were quite similar, ranging from  $r = 0.733$  to 0.745. The total range of correlations across all 100 trials varied by less than 2% (0.012), with a standard deviation of 0.004. The 2% range in correlation values is small enough to reject this null hypothesis and to affirm that our  $k$ -means cluster assignment protocol is rather insensitive to variation in starting seed values.

The second null model assumed the diversity of any grid cell was merely the result of source pool effects, meaning that the alpha diversity of a grid





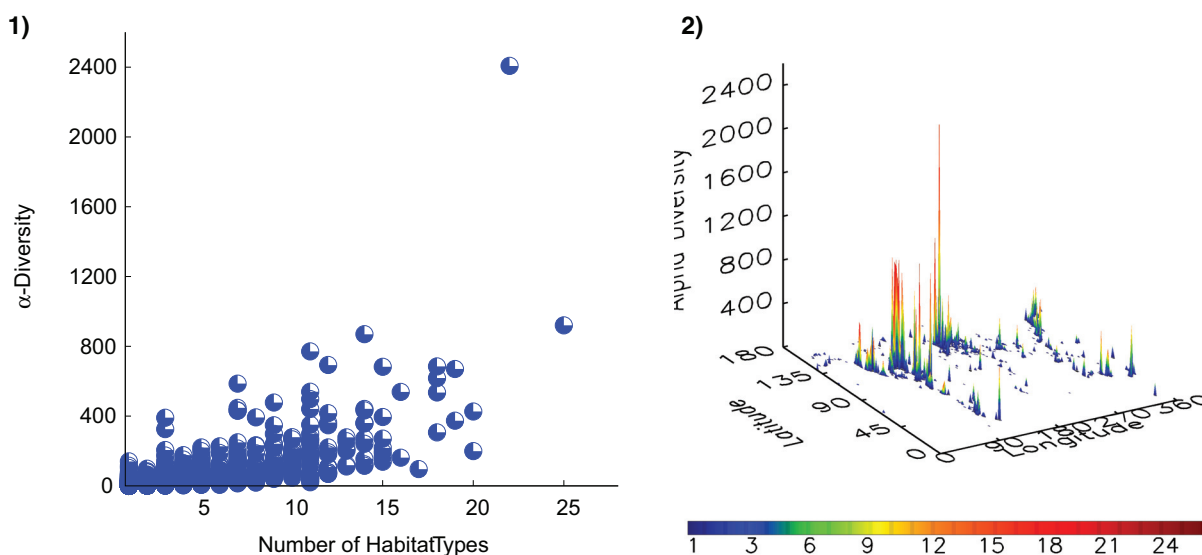
**FIGURE 3.** Total alpha diversity by region (57Ma–present). These show that eastern North America is the most diverse region. The alpha diversity of grid cells are indicated by the colors plotted on the map. Hot colors (red) correspond to high alpha diversity. North America 3.1) contrasts strongly to Europe 3.2) and Japan 3.3).

cell should be related to the diversity of its source pool (neighborhood). We measured source pool diversity for each grid cell and tested the correlation between alpha diversity and source pool diversity. The correlation was weak ( $r = 0.341$ ), and indicates that the diversity of the average grid cell was independent of its surrounding neighborhood. Therefore, the habitat(s) of each grid cell was not necessarily bound by trends of the neighborhood at this grid cell resolution which suggests that a grid cell can respond to environmental forcing independent of its source pool.

## DISCUSSION

This study explored a new concept to explain observed patterns in marine biogeography during the past 57 m.y., that a proxy for the diversity of habitats is a strong predictor of the diversity of macrofossils within a grid cell. However its pertinence should be tempered by at least two considerations. First, the geographic distribution and physical size of fossils used in this study limit extrapolation of these results. These data are dominated by marine bivalves and brachiopods, which although useful as a model for macroevolutionary





**FIGURE 4.** 4.1) Scatter plot of alpha diversity and the diversity of  $k$ -means habitat types illustrating the strength of this relationship ( $r = 0.763$ ). 4.2) Global diversity landscape map. The alpha diversity of the entire globe for the most recent 57 m.y. is given by amplitude along the vertical axis, and the fourth dimension of habitat type diversity is given by the color of the peaks. Notice that most tall peaks are also hot colors, which highlights the linear relationship between alpha and habitat type diversity. Longitude ranges from  $0^\circ$  ( $180^\circ$  W) to  $360^\circ$  ( $180^\circ$  E), and latitude from  $0^\circ$  ( $90^\circ$  S)  $180^\circ$  ( $90^\circ$  N).

studies, are subject to bias themselves stemming from several sources including shell preservation, small size, life habit, narrow geographic extent (Valentine et al. 2006).

Second, it should be acknowledged that although we developed a rigorous protocol the relationship between diversity and habitat type is particularly sensitive to the quality of the PD's lithological annotations (Peterson and Nakazawa 2008) and their translation from categorical to scalar quantities (see Appendix Tables 1, 2). It seems likely that the conversion of categorical data to mean scalar values (e.g., siltstone to 0% sand, 83.3% silt and 16.7% clay) may be too general to capture some subtler details necessary to distinguish, for example, siltstone deposition that occurs in different environments.

The analysis of differences in diversity measures across various tectonic settings presents an important test for our understanding of long-term biodiversity drivers. When taken over the entire period from 57 Ma to present, grid cells from eastern North America were the most diverse (Figure 3.1) despite being far removed from tectonic activity, while grid cells from tectonically active areas including Europe and Japan showed diversities that were only a fraction of that in eastern North America. Any hypothesis connecting the macrodiversity of a region to its tectonism should also

account for these elevated diversities in passive regions.

On the other hand if considering only the tectonically active regions, tectonism and increased diversity did coincide with Europe and Japan where alpha diversity peaks during or near epochs of noted tectonic activity (Burbank et al. 1992; Takahashi and Saito 1997; Hall 2002, Vergés et al. 2002). Japan's grid cell diversity peaked during the Miocene, a phase of probable accelerated plate motion in the area, during a continuum of tectonism there. Europe's grid cell diversity peaked during the Eocene, which also was a period of tectonic activity.

When both passive and active tectonic regions are both considered the variability in the number of habitat types, as determined through the diversity of lithologies present within a grid cell correlates reasonably to variability in diversity (species level:  $r = 0.763$ ). We should, however, note that other relationships have a strong bearing on the overall biodiversity of an area. Particularly well observed are latitudinal gradients in biodiversity. We limited some latitudinal influence by constraining our analysis to regions of similar latitudinal zones. Our regions of eastern North America, Europe, and Japan are located between  $25^\circ$  and  $60^\circ$  north latitude.

**TABLE 4.** Species level correlations. Each column lists the Pearson correlations,  $r$ , for alpha diversity and beta diversity. Values in parentheses correspond to correlations with rarefied diversity. All correlations are significant ( $P > 0.001$ , two-tailed test), except alpha diversity:mean depth, and beta diversity:mean depth, mean sand, silt, and clay pct. 4 Species level correlations. Each column lists the Pearson correlations,  $r$ , for alpha diversity and beta diversity. Values in parentheses correspond to correlations with rarefied diversity. All correlations are significant ( $P > 0.001$ , two-tailed test), except alpha diversity:mean depth, and beta diversity:mean depth, mean sand, silt, and clay pct.

Parameter	Alpha Div. (Rarefied Div.)	Beta-Div. (Rarefied Div.)
Hab. Type Div.	0.763 (0.679)	-0.133 (0.193)
Connectivity	0.285 (0.338)	0.632 (0.686)
Mean Depth	-0.009 (-0.013)	0.030 (-0.119)
Depth Range	0.271 (0.134)	0.088 (0.076)
Mean Sand Pct.	0.089 (0.173)	0.132 (0.038)
Mean Silt Pct.	0.004 (0.208)	-0.004 (-0.068)
Mean Clay Pct.	0.040 (0.134)	-0.053 (0.105)
Mean Lime Mud Pct.	0.041 (0.104)	-0.029 (0.199)

We also considered that sampling resolution (grid cell size), such as was examined by Mac Nally et al. (2004), could alter the strength of the habitat type-alpha diversity relationship studied here. Sufficiently large grid cells would contain homogenized communities with low beta diversities while much smaller communities would appear more heterogeneous with higher beta values. We recognized the trade-off between grid cell size and geographic uncertainty, and our choice of a  $1^\circ$  by  $1^\circ$  resolution was based on the limitations of geographic resolution of coordinates from the PD. Tests using a data set with greater geographical resolution than was used here, could vary the grid cell sizes and may reveal a decreasing habitat type-alpha diversity  $r$  value with decreasing grid cell size.

In summary, the results of our study of variability in the diversity of macrofossils in passive and active tectonic settings are consistent with ecological niche theory. Tectonic plate movements are complex and can be the bearers not only of biodiversity reduction, but also biodiversification through the creation of new colonizable ecospace. Mild disturbance such as periodic eruptions or forest fires would provide for the often observed effect of increasing biodiversity, as is observed in successional forests subject to wildfire. Such disturbance events in eastern North America might have influenced biodiversity there just as effectively as volcanic disturbance events during the Eocene in the Mediterranean. An important challenge for any biodiversity-tectonic hypothesis should be to explain

why tectonic disturbances should be better agents of biodiversification than disturbance events in passive areas. Our results indicate that drivers of biodiversity in passive tectonic environments are at least as effective as biodiversity drivers in convergent tectonic settings.

Our data are based on 83,213 fossil occurrences that were partitioned into 1,565 spatially equivalent grid cells, which spanned the most recent 57 m.y. These data indicate that the most robust predictor of alpha diversity (at genus or species level) in both passive and active tectonic settings is the number of habitat types which is consistent with modern ecological observations where diversification occurs as a response to limitations, and species tend to specialize and diversify as they partition themselves along resource gradients.

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