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Diversity and Community Structure of Marine Invertebrate Fossil Assemblages from the Neogene of the Dominican Republic

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DIVERSITY AND COMMUNITY STRUCTURE OF MARINE INVERTEBRATE FOSSIL ASSEMBLAGES FROM THE NEOGENE OF THE DOMINICAN REPUBLIC

A Thesis

Presented to

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San José State University

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of the Requirements for the Degree

Master of Science

By

Nina Abdollahian

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The Designated Thesis Committee Approves the Thesis Titled

DIVERSITY AND COMMUNITY STRUCTURE OF MARINE INVERTEBRATE FOSSIL ASSEMBLAGES FROM THE NEOGENE OF THE DOMINICAN REPUBLIC

by

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APPROVED FOR THE DEPARTMENT OF GEOLOGY

SAN JOSÉ STATE UNIVERISTY

December 2015

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ABSTRACT

DIVERSITY AND COMMUNITY STRUCTURE OF MARINE INVERTEBRATE FOSSIL ASSEMBLAGES FROM THE NEOGENE OF THE DOMINICAN REPUBLIC

by Nina Abdollahian

River valleys in the Cibao Valley Basin, located in the northern Dominican Republic, expose three fossiliferous Neogene-aged strata (the Cercado, Gurabo, and Mao formations) that show evidence for shifting marine paleo-habitats. This study system is ideal for analyzing the relationships between environmental changes and faunal community stability through time. A new database was developed from the published literature to examine changing diversity patterns and to determine if the Cibao Valley communities exhibited stasis over a 3 My time span (6.5 Ma to 3.5 Ma) across shallow- to very deep-water environments. This database includes spatio-temporal occurrence data for 179 species of gastropods, bivalves, and corals. Analyses of diversity patterns reveal a high diversity of species in shallow- to deep-water depths, and a low diversity of species in very deep-water depths, as well as a low similarity of species through time across the different paleoenvironmental settings. An R-mode hierarchical cluster analysis illustrates two major clusters that were based mostly on the different paleoenvironments in which these species lived, while a Q-mode cluster analysis shows two major clusters, one consisting mostly of mollusk and the other of corals. Finally, a detrended correspondence analysis indicates higher species richness in intermediate-water depths and lower species richness in very deep-water depths. In total, these results indicate faunal instability though changing habitats across time in this study system.

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Table of Contents

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

The Cibao Valley Basin, located in the northern Dominican Republic, was an open shelf marine habitat millions of years ago and has been evolving for the past 10 My. As a result of tectonic uplift, the valley basin has exposed deposits of Neogene marine sediments that record shifting environments and include an abundance of invertebrate fossils, especially corals, mollusks, bryozoans, and various microfossils (McNeill *et al.*, 2012, Saunders *et al*., 1986). Aspects of this fauna have been studied by various authors and, as a result of their work, 23 monographs have been published in the *Bulletins of American Paleontology* (Table 1). These monographs describe the fossils, including where they were found, geographically and stratigraphically, as well as the geology of the region. The collection localities include river cuts (Río Cana, Río Gurabo, Río Mao, Río Amina, Cañada Zalaya, Río Yaque del Norte, Arroyo Puñal, and Río Verde) and the City of Santiago, as well as several road cuts (Fig. 1).

The main purpose of this study is to use the spatio-temporal occurrence data associated with Dominican fossils collected from Neogene strata exposed by two rivers, Río Gurabo and Río Cana, to investigate the diversity and community stability of bivalve, gastropod, and coral species across different environmental settings over time. Community stability in this study system could indicate that species are able to gradually adapt to the changing ecosystem over a 3 My time span, while instability in the study area would indicate that species within these communities could not adapt to environmental shifts over time.

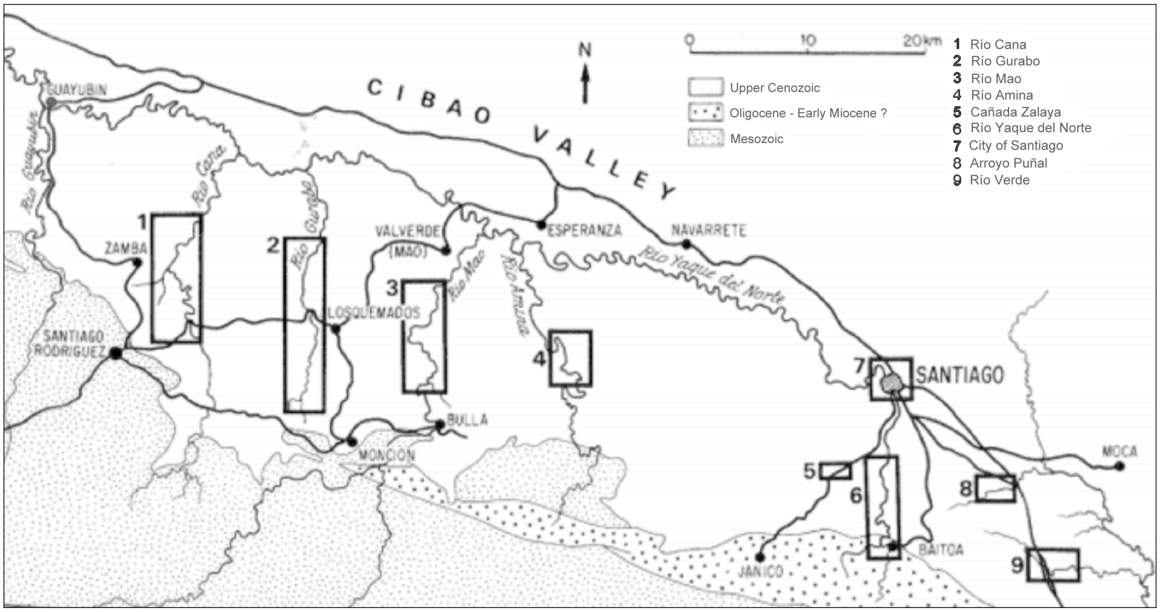


Figure 1. Cibao Valley Basin, located in the northern Dominican Republic, and the nine rivers where samples were collected (Modified from Text-Figure 3 from Saunders *et al*. 1986; reproduced with permission from the Paleontological Research Institution, Ithaca, New York).

OVERVIEW OF FORMATIONS IN STUDY SYSTEM

Three Neogene formations are exposed along nine rivers and road cuts in the Cibao Valley Basin: the late Miocene Cercado Formation, the early Pliocene Gurabo Formation, and the middle Pliocene Mao Formation. Each formation provides evidence of Neogene sea level fluctuations that occurred in the Cibao Valley Basin. The following overview is summarized from the recent review in McNeill *et al.* (2012).

The Cercado Fm. shows evidence for the first flooding in the Cibao Valley Basin around the Late Messinian (6.6-6.0 Ma), as evidenced by inner shelf sand deposits. As a result of the flooding and with an addition of ideal conditions (including high temperature and salinity, as well as low nutrient supply), coral reefs flourished in the Cibao Valley

Basin during the deposition of this unit. The Cercado Fm. also shows evidence for a period of major sea level decline during the end-Messinian, as evidenced by coral reef deposits buried by siliciclastic material.

The early Pliocene Gurabo Fm. shows evidence of sea level oscillations between 5.6-4.0 Ma. The Gurabo Fm. records a transgressive period that led to an increase in sea level at about 5.3 Ma. Around 5.1 Ma, sea level fell and disturbed the normal marine conditions. Finally, during the late-early Pliocene, the occurrence of the foraminiferan *Globorotalia margaritae* showed evidence of warming and an increase in sea level in this study system.

The mid-Pliocene Mao Fm. shows evidence for a cycle of sea level rise and seaward progradation followed by a disconformity, which marks a period of sea level lowstand. These cycles are signified by the “mixed silt, sand, and coarse siliciclastic material … that transition … to interbedded coral and silt beds” (McNeill *et al.,* 2012, p. 56), while the sea level drop is marked by coarse sand, gravel deposits, and a thick layer of marine deposits that include fossils. The sea level drop may have been a result of increased northern and southern hemisphere glacial activity, along with uplift of the Cordillera Central and Cibao Basin (McNeill *et al*., 2008). Finally, during the late Pliocene, the accumulation of marine deposits declined in the Cibao Valley Basin. This decline was due to the shallowing of the basin coupled with regional uplift, which restricted the Cibao Valley Basin, and also led to a sea level lowstand in the area (Fig. 2) (McNeill *et al.,* 2008).

Table 1. The twenty-four taxonomic monographs published in the *Bulletins of American Paleontology* used to construct the core dataset analyzed in this study.

Series Number	Author (Year)	Taxon
1	Saunders, J., Jung P. and Biju-Duval B. (1986)	Field survey, lithology, environment, and age
2	Jung, P. (1986)	Genus *Strombina* (gastropod)
3	Foster, A.B. (1986)	Family Poritidae (coral)
4	Foster, A.B. (1987)	Genus *Stephanocoenia* (coral)
5	Cairns, S.D. and Wells J.W. (1987)	Suborders Caryophylliina and Dendrophylliina (coral)
6	Logan, A. (1987)	Phylum Brachipoda (brachiopod)
7	Van den Bold, W.A. (1988)	Subclass Ostracoda (Crustacea)
8	Vokes, E.H. (1989a)	Family Muricidae (gastropod)
9	Vokes, H.E. (1989b)	Family Cardiidae (bivalve)
10	Jung, P. and Petit R.E. (1990)	Family Cancellaridae (gastropod)
11	Budd, A.F. (1991)	Family Faviidae (Part I) (coral)
12	Vokes, H.E. and Vokes E.H. (1992)	Genus *Spondylus* (bivalve)
13	Kier, P.M. (1992)	Class Echinoidea (sea urchin)
14	Nolf, D. and Stringer G.L. (1992)	Otoliths of telestean fishes

Series Number	Author (Year)	Taxon
15	Jung, P. (1994)	Genera *Columbella, Eurypyrene, Parametaria, Conella, Nitidella,* and *Metulella* (gastropod)
16	Anderson, L.C. (1996)	Family Corbulidae (bivalve)
17	Jung, P. (1996)	Families Cuspidariidae and Verticordiidae (bivalve)
18	Vokes E.H. (1998)	Superfamily Volutacea (gastropod)
19	Budd, A.F. and Johnson K.G. (1999)	Family Faviidae (Part II) (coral)
20	Stemann, T.A. (2000)	The Family Agariciidae (coral)
21	Nehm, R.H. (2001a)	Genus *Prunum* (gastropod)
22	Costa, F.H.A., Nehm R.H. and Hickman C.S. (2001)	Family Neritidae (gastropod)
23	Freiheit, J.R. and Geary D.H. (2009)	Genera *Strombus* and *Lobatus* (gastropod)
24	Waller, T.R. 2011	Propeamussiidae and Pectinidae (bivalve)

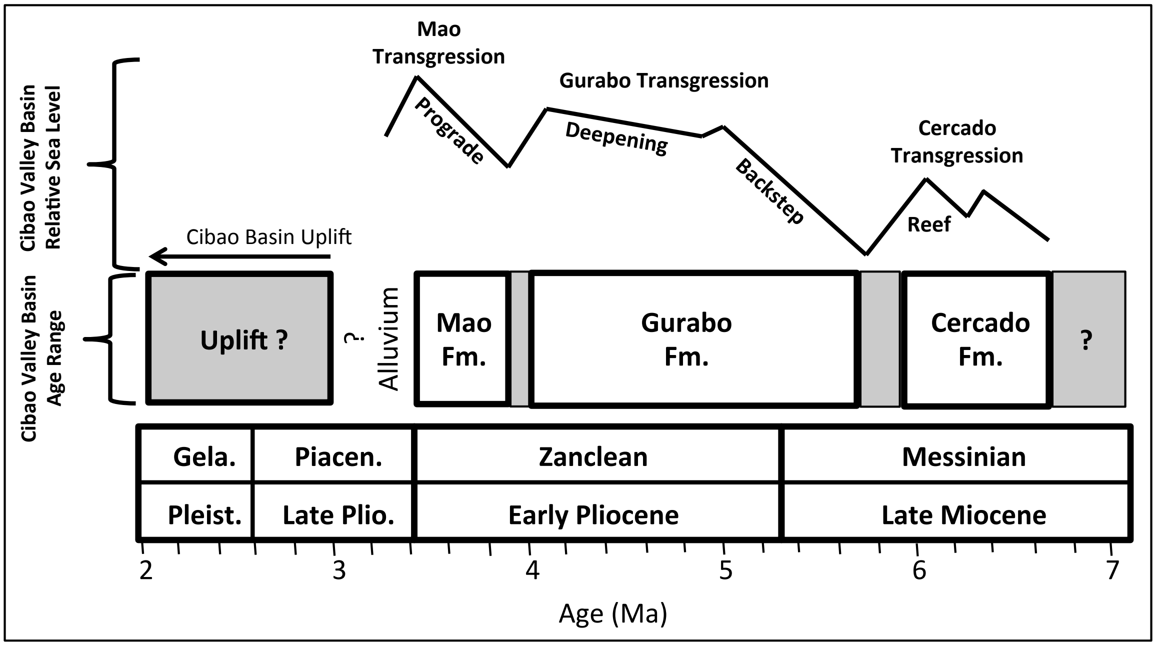


Figure 2. Paleoenvironmental changes according to depositional and relative sea-level records in the Cibao Valley Basin (Modified from fig. 15, McNeill *et al*. 2012).

PALEOECOLOGICAL STUDIES

The Cibao Valley Basin has been extensively studied due its rich abundance of Neogene fossils and evidence of shifting paleoenvironments, making this study area ideal for paleobiological research on the relationships between environmental change and faunal stability. Anderson (1994) examined how paleoenvironmental factors may have affected the distributional patterns of members of the bivalve clade Corbulidae in the Dominican Republic. One of her goals was to determine if the distributional patterns of the corbulid species are a result of speciation and extinction, or of migration. The author examined the Baitoa, Cercado, Gurabo, and Mao formations to determine the different paleoenvironments in the study area. She concluded that the Miocene deposits represent shallow marine conditions while the Pliocene deposits were deposited in deeper marine conditions. The corbulid species are eurytopic, tolerating a wide range of habitats, but favoring shallow marine waters. Corbulid species are more abundant and diverse in the Miocene than in the Pliocene deposits. Anderson's (1994) results indicate that the first appearances of the corbulids were in shallow marine deposits, and the last occurrences were correlated with deep-water sediments. The author concluded that the corbulid species distributions are correlated with paleoenvironmental oscillations, indicating that these species migrated in and out of the study area (Anderson, 1994).

Rivera *et al.* (2008) conducted a study on the variability of mollusk assemblages in the Dominican Republic. The authors focused on two stratigraphic units exposed at Río Gurabo: the Cercado Fm. (their G1) and the Gurabo Fm. (their G9). Their goal was to determine species richness patterns, and paleocommunity variation, and from there, understand the distribution and abundance patterns of more than 300 mollusk species. Rivera *et al.* (2008) found that the Gurabo Fm. has an upper and lower section, which have different species richness patterns. The bulk samples collected from the upper Gurabo Fm. had diversity ranges between 42-72 species while the samples from the lower Gurabo Fm. had 20-35 species. Additionally, when comparing species richness values to the Cercado Fm., the Gurabo Fm. has an overall larger value. Rivera *et al.* (2008) performed a Non-metric Multidimensional Scaling (NMS) analysis that showed three main faunal groupings that were organized into lithostratigraphic zones: G1 (Cercado Fm.), G9 Zone A (upper Gurabo Fm.), and G9 Zone B (lower Gurabo Fm.). Finally, by using the three faunal zones, the authors were able to identify the mollusk distributional and abundance patterns in the Río Gurabo section. Rivera *et al.* (2008)

found that only 21 species of mollusks (12 bivalves and 9 gastropods), from the 300 mollusk species analyzed, persisted from the older Cercado Fm. through the younger Gurabo Fm. Finally, within the different faunal zones (G1, G9 Zone A, and G9 Zone B) the abundance of these 21 species fluctuated but persisted through each lithostratigraphic unit (Rivera *et al*., 2008).

Klaus *et al.* (2008) investigated the community changes in coral assemblages during the Neogene in the Dominican Republic. These authors investigated whether coral communities were stable in species composition or if they changed in conjunction with environmental factors that varied over time. They studied about 4,000 coral specimens belonging to 104 species from the Cercado, Gurabo, and Mao formations. In order to study coral community variation through time, the authors focused on the coral species that were found in multiple formations, then analyzed whether each of those coral species was present or absent in each locality. In order to determine the degree of faunal stability, the authors used the Brett and Baird (1995) faunal stability minimum of 60%. The authors found that of the 104 species, 61% of them persisted from the Cercado Fm. to the Mao Fm. They concluded from their initial test that these coral communities were faunally stable through time. Additionally, they recorded fossil coral presence/absence data for the 104 species in 21 lithostratigraphic units within the three formations, and used a cluster analysis to determine the variability within the communities. Bray-Curtis similarity indices indicated two distinct assemblage types: mixed-shaped corals and free-living corals. Additionally, the cluster analysis demonstrated that the two coral assemblages were stable over the 3 My time span of the study interval. Finally, the authors used 27 20-m line transects from reef zones in Arroyo Bellaco, Cañada de Zamba, and Cana Gorge to determine the relative abundance and community stability of the species. This last test showed a decrease in similarity of branching corals and massive corals species through time. They concluded that the first two tests were broad analyses while their third test was a much more refined analysis that indicated a strong correlation between the community variation and environmental changes through time in the study system (Klaus *et al.,* 2008).

MATERIALS AND METHODS

Database

A subset of the Dominican Republic fossil record has been published in 23 taxonomic monographs written by various authors and published in the *Bulletins of American Paleontology* (Table 1). A new species-level database of Neogene marine invertebrate species was compiled from these monographs. This core database included the following elements: 1) taxon name; 2) locality code; 3) stratigraphic formation; 4) general location; and 5) georeferenced latitude and longitude points. There were two types of localities recorded in this database: Tulane University collections (TU) and Naturhistorisches Museum Basel (NMB) collections. Google Earth (Google Inc., 2015) was used to georeference the latitude and longitude points of fossil localities that are found on river maps of Río Cana and Río Gurabo, published by Saunders *et al.* (1986).

This study focused only on records of bivalves, gastropods, and corals from Río Gurabo and Río Cana to identify potential community shifts in relation to stratigraphy.

Thus, only 20 of the 23 taxonomic monographs were used. In addition to elements from the core database, the dataset utilized in this study also included the following information for each locality: its position in the stratigraphic section (in meters above the base), its paleoenvironmental interpretation based on Saunders *et al*. (1986) and Waller (2011) (see below), and an estimate of its absolute age. Two approaches were used to determine the stratigraphic position for each locality. The first approach used detailed stratigraphic sections for both Río Cana and Río Gurabo, published by Saunders *et al.* (1986), to determine an estimated (±10 m) position for each locality in the section. The second approach matched TU and NMB locality numbers to stratigraphic information from Waller (2011) and Vokes (1989a), to obtain a more precise stratigraphic position. Additionally, absolute age information for each locality was estimated using figures 10 and 12 in McNeill *et al.* (2012), which are age-depth models for Río Cana and Río Gurabo. The age information was obtained by correlating where the locality lies in the stratigraphic section relative with the absolute age information given on the age-depth model (See supplementary data).

Community stability was examined by the presence and absence of species within these communities with respect to temporal changes in the habitats. Stratigraphic occurrences were divided into six time bins (TB1-TB6), each 500,000/years in length, to allow analysis of temporal trends across 3 My of geological time (6.5 to 3.5 Ma). It is assumed that species persisted between their first and last occurrences; thus "range through" occurrences were applied to intervals in between, from which the taxon was not recovered. For example, if a sample was collected from TB1 and TB4, it must have persisted through TB2 and TB3, even if it was not collected from those time intervals. The species in Río Gurabo and Río Cana were then organized into four presence/absence matrices indicating whether a species was present or absent in each time bin, formation, and paleoenvironment (see below), as well as the river cut from which they were collected.

Paleoenvironment

This study used rock lithology and fossil assemblages as proxies to estimate paleoenvironmental conditions of individual localities. Research by Nehm (2001a), indicated that gastropods belonging to the genus *Prunum* are a good proxy for determining water depth because modern representatives favor a shallow-water seagrass habitat (also see Waller, 2011). Vokes (1989a) found that the family Muricidae is also a good indicator for water depth because some species (or closely related species) from the Neogene of the Dominican Republic are extant and have known modern depth ranges. Using these gastropods, she indicated that the Cercado Fm. was deposited in water depths that were between 0-20 m, the lower Gurabo Fm. in water depths between 20-50 m, the middle Gurabo Fm. in water depths between 50-150 m, the upper Gurabo Fm. in water depths between 150-350 m, and the Mao Fm. in water depths below 350 m. Waller's (2011) research on scallops in the Cibao Valley Basin was also especially helpful in reconstructing the paleo-habitats. Waller recognized five ecological settings (shallow shelf, middle to outer shelf, outer shelf edge, mud bottoms, and coral reef and carbonate sediments) and he characterized them based on the Propeamussiidae and Pectinidae scallop assemblages present. These assemblages represent fluctuating water depths, habitat changes on the sea floor, and evidence of coral reefs or marine grasses and algae (Waller, 2011). The Propeamussiidae and Pectinidae assemblages were used instead of the Muricidae species to determine the paleoecological settings within the Cercado, Gurabo, and Mao formations because the assemblages described by Waller (2011) provided more information on the paleo-habitats of individual localities.

Data Analysis

The relationship between species persistence through time and environmental change was examined with a gridded heat map based on presence/absence data (Wilkinson *et al.*, 2008). Each row on the heat map represents a species, and each column represents a collection locality; the colors indicate the presence or absence of each species within each locality. Total species count (richness) in the analyzed groups was calculated in order to identify how the diversity of species changed through different time intervals (6.5 Ma to 3.5 Ma) and environments (shallow- to deep-water).

The Jaccard similarity coefficient (S_J) (Real and Vargas, 1996) was used to measure the similarity in species composition across the three formations.

$$S_j = \frac{C}{A+B-C}$$

where A is the number of species in the first formation only, B is number of species in the second formation only, and C is number of species in both formations

The Jaccard similarity coefficient is a value between 0 and 1, 0 representing least similarity in species composition and 1 representing absolute similarity. If, for example, the Jaccard similarity coefficient is 0.3 for species at boundary 1 (between two formations) then there is a low similarity of species between the formations. On the other hand, if the Jaccard similarity coefficient is 1 for species at boundary 2, then species have absolute similarity between the formations.

Hierarchical cluster analysis (Hammer and Harper, 2006) was used to evaluate the distribution of species through time and across different paleoenvironmental settings. Euclidian distance (Hammer and Harper, 2006) was used as a measure of species composition dissimilarity between pairs of samples. Clusters were created using the average linkage, paired group algorithm (Hammer and Harper, 2006). Two types of cluster analyses were conducted for this study: 1) an R-mode clustering, where the columns of the database represent taxa; and 2) Q-mode clustering, where the columns of the database represent samples. The R-mode cluster analysis represents how the sampling areas are related based on the co-occurrence of taxa, while the Q-mode cluster analysis represents how the taxa are related based on their co-occurrence in the sampling areas. The localities for the cluster analyses were broken up into the six different time bins for Río Gurabo (RG1-RG6) and Río Cana (RC1-RC6) as described above. Río Gurabo does not have any samples representing TB5.

Finally, relationship between paleoenvironmental factors and species composition were examined with a Q-mode Detrended Correspondence Analysis (DCA) (Hammer and Harper, 2006) to illustrate how the species cluster by water depth. The detrending method was used to better represent the distribution of species along a paleoenvironmental gradient. These last two methods, hierarchical cluster analysis and DCA, were conducted using PAST v3.0 (Hammer and Harper, 2006).

RESULTS

Overview of Dataset

The database used for this study includes spatio-temporal occurrence information from 179 species of gastropods (88 species, 7 families), bivalves (53 species, 5 families), and corals (38 species, 4 families), which were collected from 309 different localities; these occurrences are summarized in Figure 3. The bivalve family Pectinidae (23 species), gastropod family Muricidae (42 species), and the coral family Faviidae (24 species) are the most species-rich families in this database. The highest total number of species (n=93) existed between 5.5 Ma and 5.0 Ma (TB3), while the lowest total number of species (n=2) existed between 4.5 and 4.0 Ma (TB5) (Table 2). The low species count in TB5 may be due to a sampling bias owing to a lack of preserved fossils of that age in the locality area. Thus, the majority of the species recorded from TB5 are "range through" occurrences (Fig. 4).

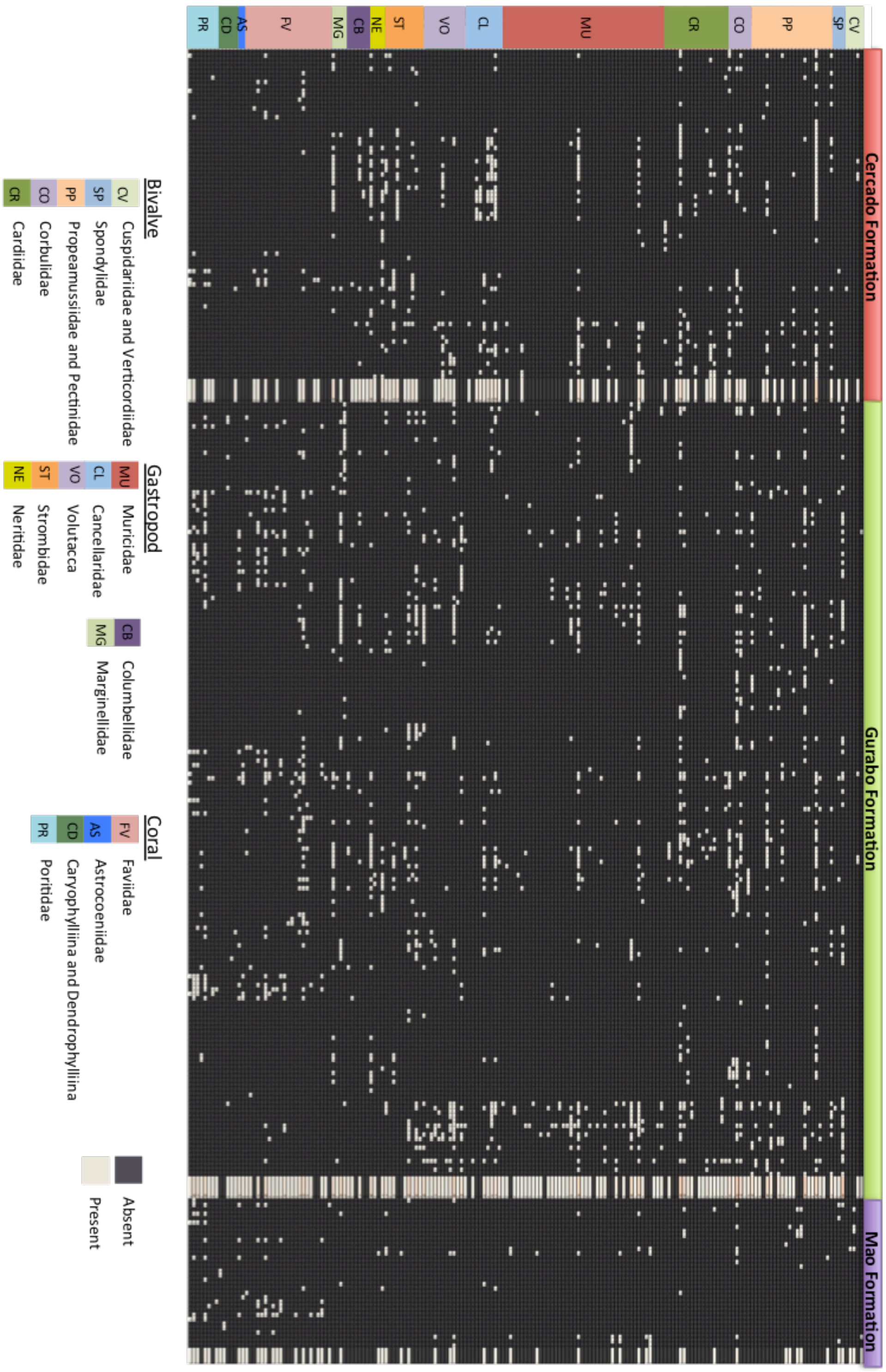


Figure 3. Heat map showing species persistence through the three formations. Each column represents a fossil locality and each row represents a species within each family.

Table 2. Species counts and Jaccard similarity coefficient comparing values for each time bin from Río Gurabo and Río Cana, not including "range through" data.

Time Bin	Río Gurabo: Species Count	Río Cana: Species Count	Total Number of Species	Jaccard Similarity Coefficient
6	51	37	54	**0.63**
5	2	2	2	**1.00**
4	91	67	91	**0.74**
3	80	83	93	**0.75**
2	82	77	89	**0.79**
1	72	82	90	**0.71**

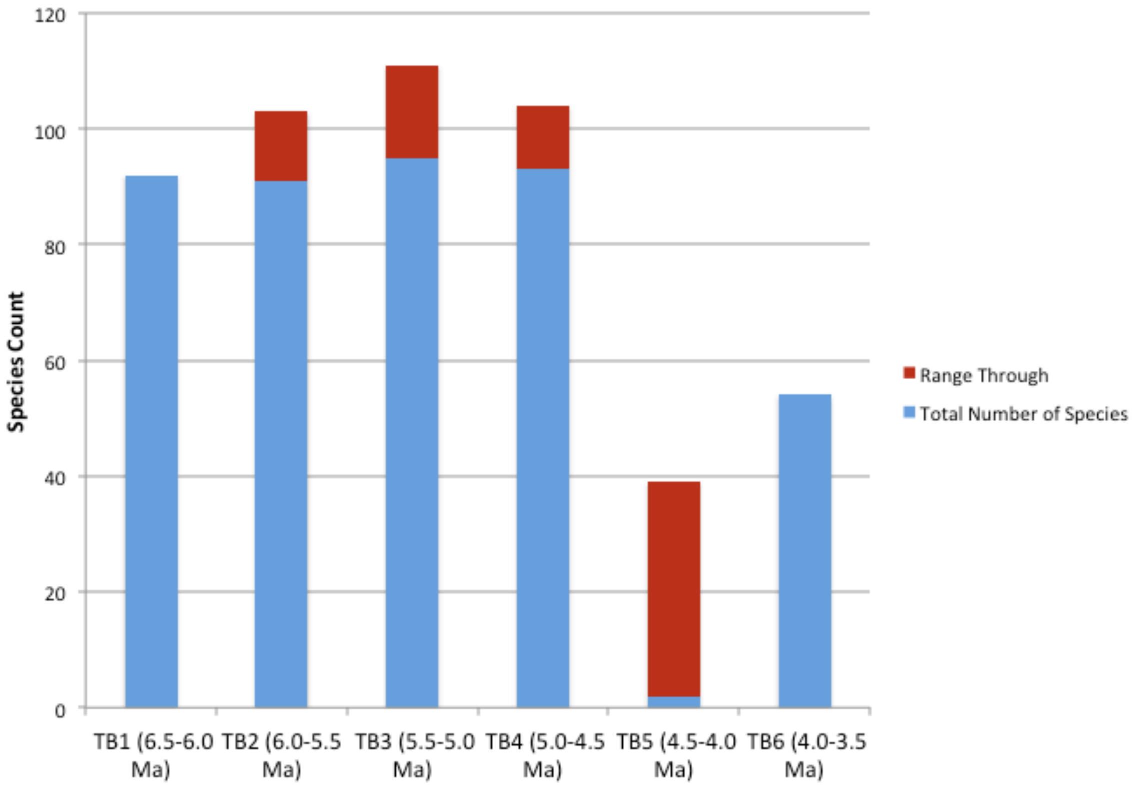


Figure 4. Summary of diversity patterns between 6.5 Ma to 3.5 Ma from Río Gurabo and Río Cana, including diversity levels with and without "range through" occurrences.

Diversity

Species diversity was lowest in deep-water habitats and highest in the habitats representing intermediate-water depths. The Gurabo Fm., which represents intermediate-water depth, had the highest diversity of species (n=143) while the Mao Fm., which represents very deep-water, had the lowest diversity of species (n=56) (Fig. 5). This pattern is also observed in the time bin data, with TB1 to TB4 showing greater diversity than TB5 to TB6 (Fig. 6).

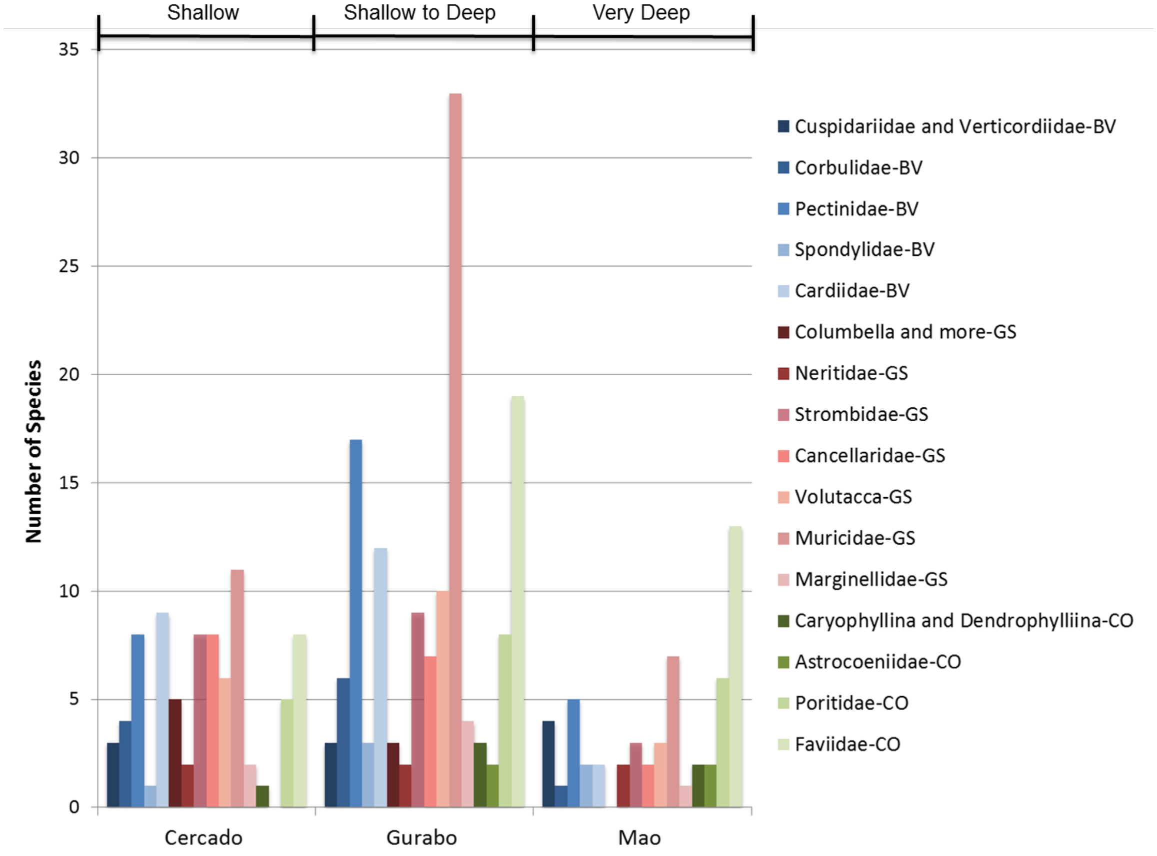


Figure 5. Changes in diversity within the three formations and across different paleoenvironmental settings represented by total number of species in each formation from both Río Gurabo and Río Cana, including range through data: Cercado Fm., 82 species; Gurabo Fm., 143 species; and Mao Fm., 56 species

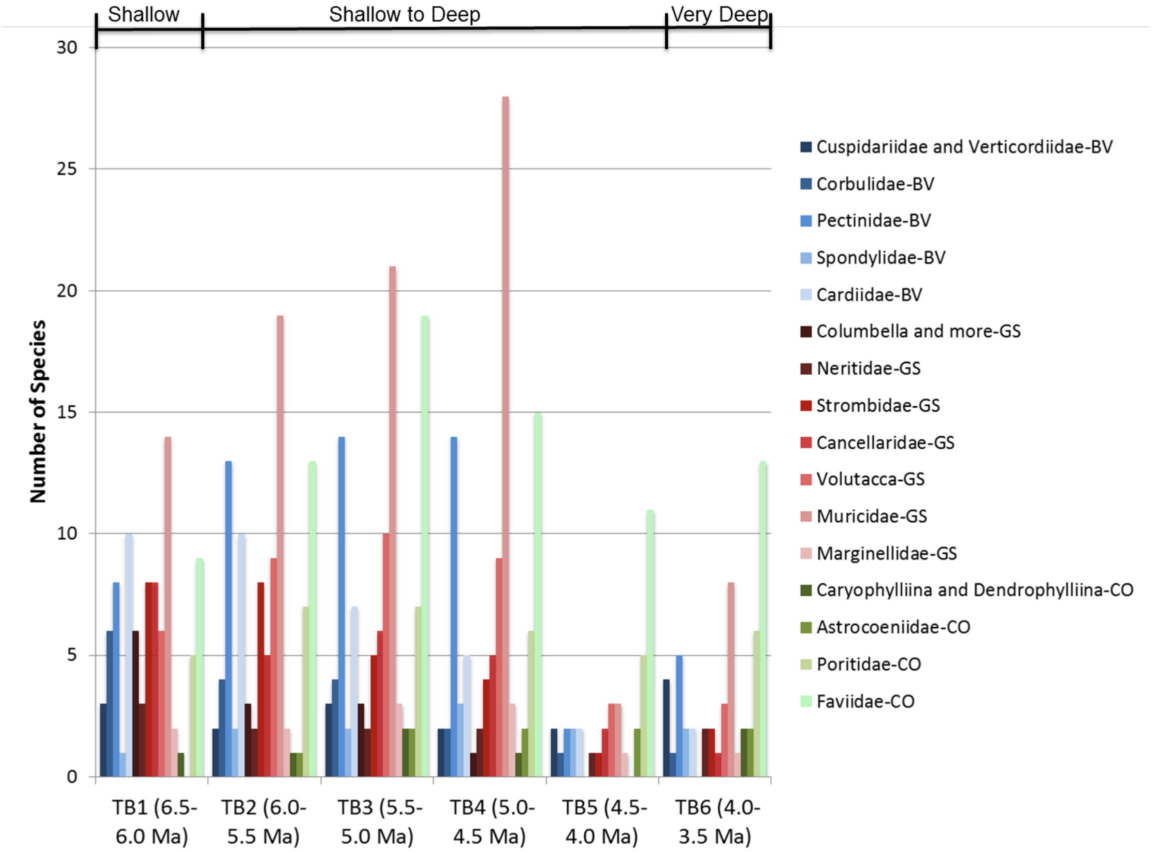
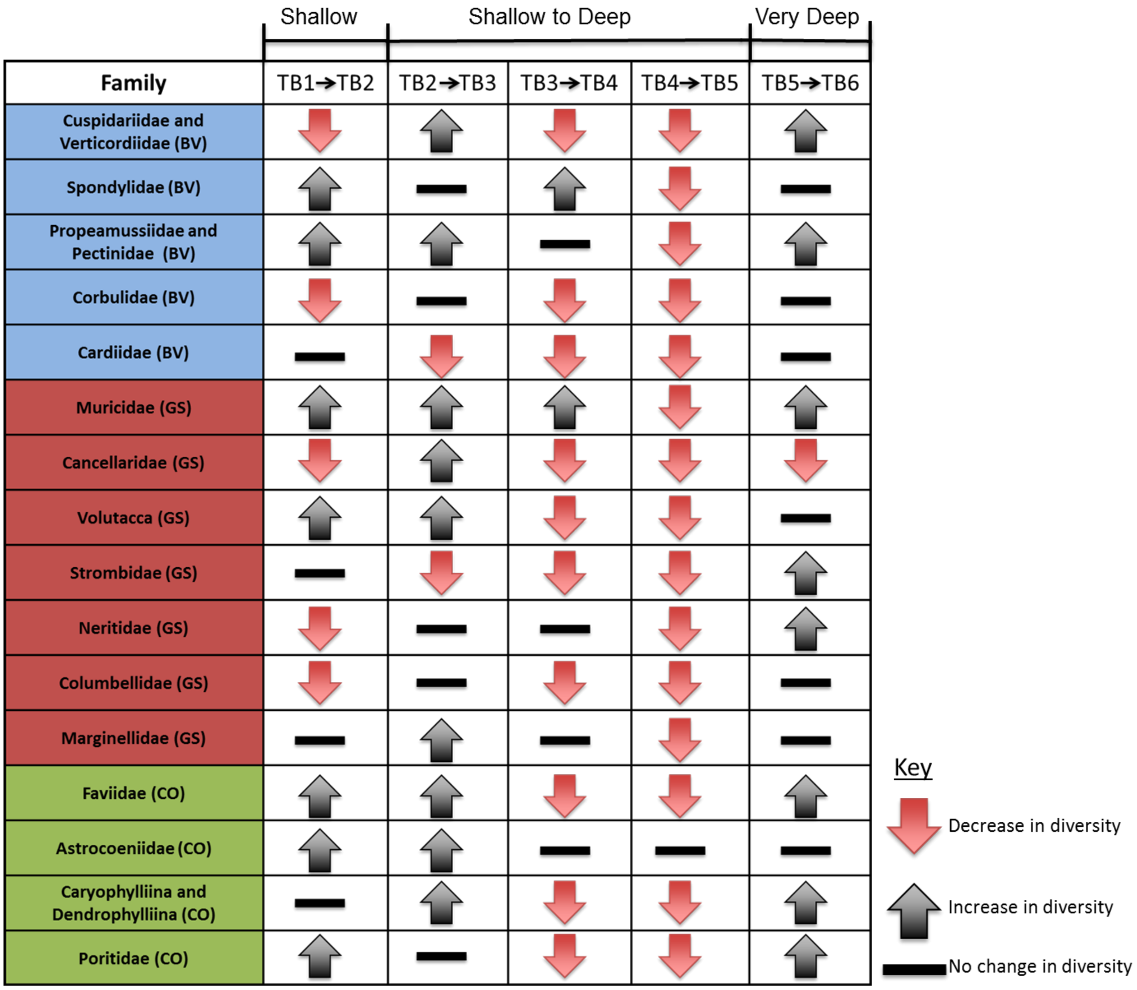


Figure 6. Changes in diversity over time and across different paleoenvironmental settings represented by the total number of species in each time bin from both Río Gurabo and Río Cana, including range through data: TB1, 90 species; TB2, 101 species; TB3, 110 species; TB4, 102 species; TB5, 38 species; and TB6, 54 species.

Figure 7 illustrates the changes in diversity of each family through time. Between 6.5 Ma and 5.5 Ma (TB1 and TB2), during shallow-water conditions, the coral families Faviidae, Astrocoeniidae, and Poritidae increased in diversity, while Caryophylliina and Dendrophylliina species had no change in diversity. The mollusk family Muricidae and superfamily Volutacea increased in diversity, while the Strombidae and Marginellidae families had no change and the Cancellaridae, Neridae, and Columbellidae decreased in diversity. On the other hand, between 6.0 Ma and 5.0 Ma (TB2 and TB3), during shallow- to deep-water conditions, all of the coral families except

Poritidae increased in diversity (the diversity of Poritidae species remained the same). Additionally, during this interval the mollusk family Muricidae and superfamily Volutacea increased in diversity, while the diversity of the Strombidae and Marginellidae families stayed the same, and the Cancellaridae, Neritidae and Columbellidae decreased in diversity (Fig. 7). From 5.5 Ma to 4.5 Ma (TB3 to TB4), the mollusk families either decreased in diversity or stayed the same, with the exception of two families, Spondylidae and Muricidae, which increased in diversity. In addition, between 5.0 Ma to 4.0 Ma (TB4 to TB5) all families decreased in diversity with the exception of Astrocoeniidae, which stayed the same. Finally, between 4.5 Ma to 3.5 Ma (TB5 to TB6) there was either no change in diversity or an increase in diversity for all families with the exception of the family Cancellaridae, which decreased in diversity. The average temporal duration of the species in the five bivalve families (1.42 My) and seven gastropod families (1.43 My) are similar through time, while the species in the four coral families (1.72 My) have a slightly higher average duration.



	Shallow	Shallow to Deep			Very Deep
Family	TB1→TB2	TB2→TB3	TB3→TB4	TB4→TB5	TB5→TB6
Cuspidariidae and Verticordiidae (BV)	↓	↑	↓	↓	↑
Spondylidae (BV)	↑	—	↑	↓	—
Propeamussiidae and Pectinidae (BV)	↑	↑	—	↓	↑
Corbulidae (BV)	↓	—	↓	↓	—
Cardiidae (BV)	—	↓	↓	↓	—
Muricidae (GS)	↑	↑	↑	↓	↑
Cancellaridae (GS)	↓	↑	↓	↓	↓
Volutacca (GS)	↑	↑	↓	↓	—
Strombidae (GS)	—	↓	↓	↓	↑
Neritidae (GS)	↓	—	—	↓	↑
Columbellidae (GS)	↓	—	↓	↓	—
Marginellidae (GS)	—	↑	—	↓	—
Faviidae (CO)	↑	↑	↓	↓	↑
Astrocoeniidae (CO)	↑	↑	—	—	—
Caryophylliina and Dendrophylliina (CO)	—	↑	↓	↓	↑
Poritidae (CO)	↑	—	↓	↓	↑

Key

↓ Decrease in diversity

↑ Increase in diversity

— No change in diversity

Figure 7. Summary of diversity changes through time including "range through" data.

Community Stasis

The Jaccard similarity coefficient results showed, on average, a low similarity of species among the three formations, which indicated community instability in the study area (Fig. 8).

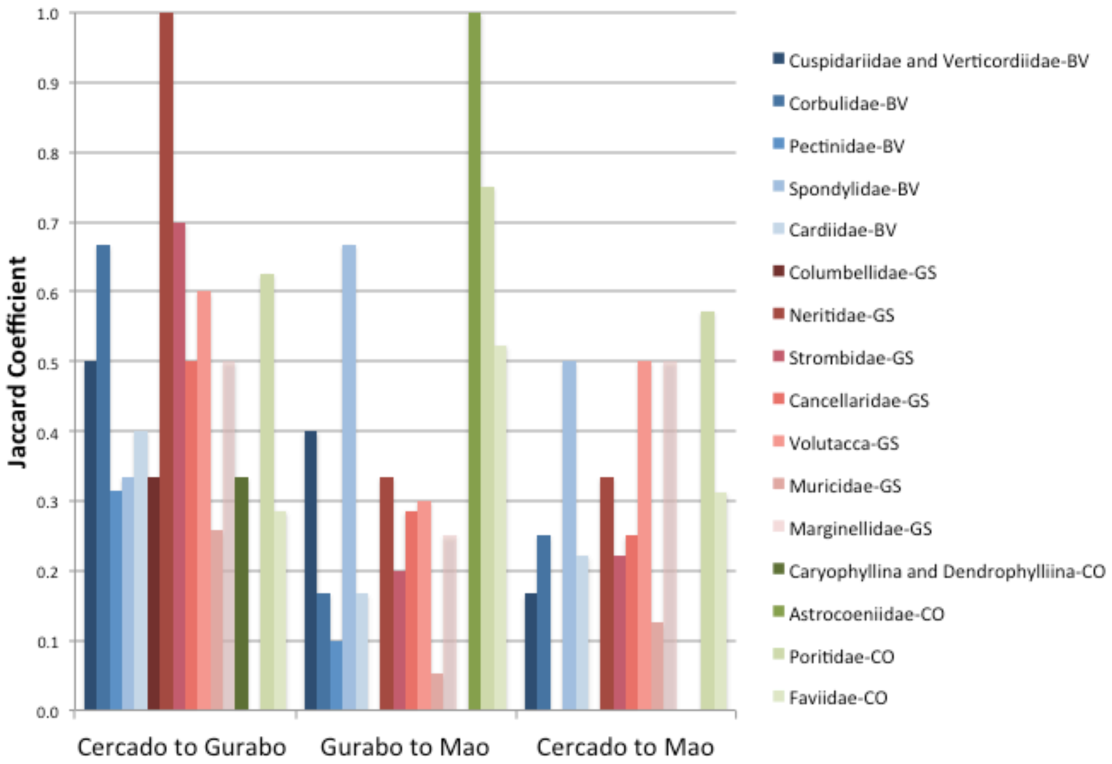


Figure 8. Comparison of Jaccard similarity coefficient between the Cercado, Gurabo, and Mao formations for the 16 families of bivalves, gastropods and corals.

The species from the five bivalve families (avg. S_J=0.44; range = 0.32-0.67), seven gastropod families (avg. S_J=0.56; range = 0.26-1.00), and four coral families (avg. S_J=0.31; range = 0-0.63) have on average a low similarity from the Cercado Fm. to the Gurabo Fm. Likewise, the species from the bivalve (avg. S_J=0.30; range = 0.10-0.67), gastropod (avg. S_J=0.20; range = 0-0.33), and coral families (avg. S_J=0.57; range = 0-1.00) have on average a low similarity from the Gurabo Fm. to the Mao Fm. Finally, the average similarity of species from the bivalve (avg. S_J=0.23; range = 0-0.50), gastropod (avg. S_J=0.28; range = 0-0.50), and coral (avg. S_J=0.22; range = 0-0.57) families between the Cercado Fm. and the Mao Fm. is low. Of the 179 species only 14% persisted from the Cercado Fm. to the Mao Fm.

Hierarchical cluster analysis showed that species richness was higher in shallow- to deep-water environments and lower in very deep-water environments. The R-mode Cluster 1 represents a shallow- to deep-water environment (TB1 to TB4), while Cluster 2 represents a predominantly deep-water environment (TB4 to TB6), with the exception of one basally branching shallow-water grouping (RG1) (Fig. 9). The Q-mode analysis also generated two large clusters; Cluster 1 included almost all the mollusk species (n=137), and a total of 23 coral species, while Cluster 2 included 14 coral species and 4 mollusk species (Fig. 10).

The DCA revealed that more species were found in intermediate-water depths rather than shallow- or deep-water depths through time. The DCA results were separated into three groups, which are highlighted as shallow, intermediate, and deep (Fig.11). These groups were divided by hand based on the time intervals, which represent the different habitats. According to this analysis, there were more species found in the intermediate-water depths and fewer found in the deep-water environments. Additionally, the deep-water habitat showed evidence for shallow-water species, which may be a result of transportation (see discussion below).

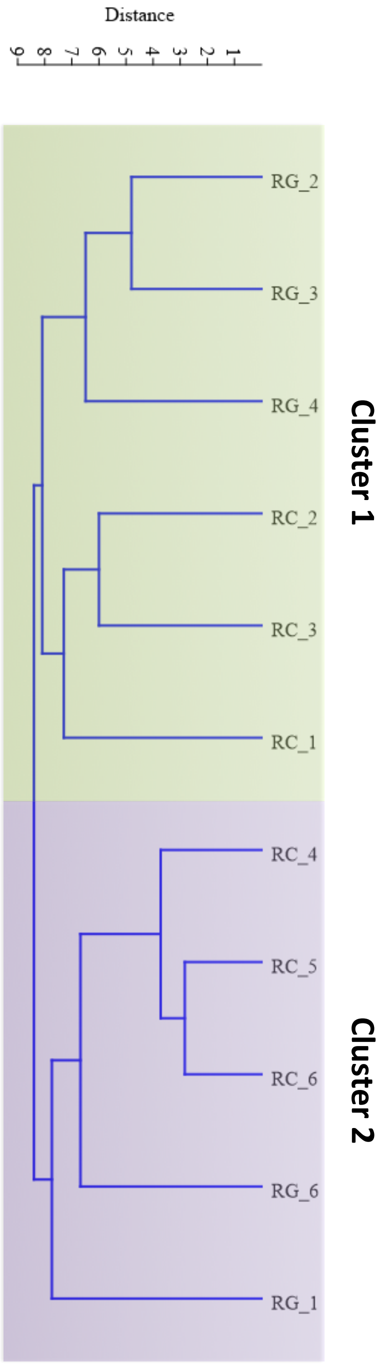


Figure 9. Dendrogram of an R-mode hierarchical cluster analysis; sample groupings are based on the Euclidian distance measurement. Cluster 1 represents a shallow- to deep-water environment and Cluster 2 represents a deep-water environment. RG= Río Gurabo; RC= Río Cana. Numbers refer to time bins 1-6.

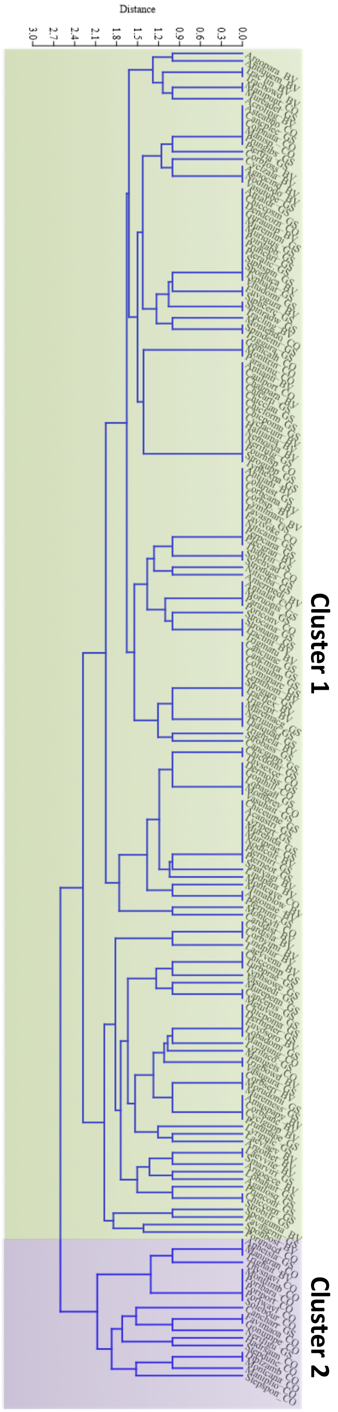


Figure 10. Dendrogram from a Q-mode hierarchical cluster analysis; groupings are based on the Euclidian distance measurement. Cluster 1 represents shallow- to deep-water species and Cluster 2 represents deep-water species. See Plate 1 for more detail.

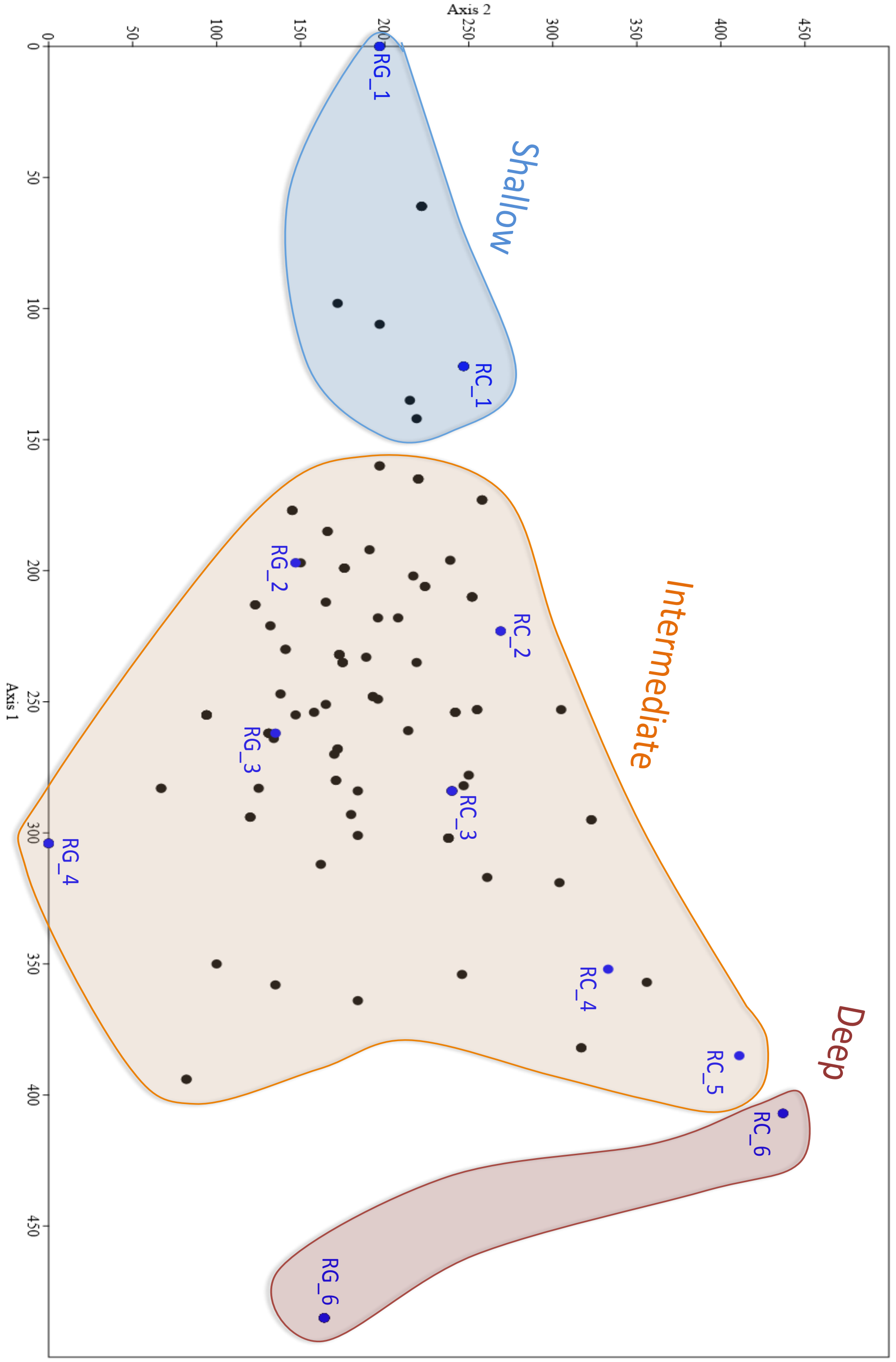


Figure 11. Results of the detrended correspondence analysis (DCA). Blue dots represent RG1-RG6 and RC1-RC6 while the black dots represent species. The shallow-water cluster incorporates RG1 and RC1, while the intermediate cluster incorporates RC2, RG2, RG3, RC4, RG4, and RC5. The deep cluster encompasses RC6 and RG6.

DISCUSSION

Diversity

The paleontology and geology of the Cibao Valley Basin has been thoroughly studied, but a comprehensive analysis of diversity and paleoecological patterns within this region has yet to be undertaken, in part because systematic studies for many groups have not yet been completed. Furthermore, the database created for this study does not include species abundance, without which any analysis of diversity will be limited. However, this study does show a pattern of species-level diversity change over time and across different paleoenvironmental settings. There is a clear decline in species diversity from 5.0 Ma to 4.0 Ma in all families (Fig. 6). This decline may be a result of the sampling bias in the 4.5 Ma to 4.0 Ma time interval. The majority of this time interval consists of "range through" data, as only two species were collected within this span of time, and only 20% of the species persist from 5.0 Ma to 3.5 Ma (Fig. 4). Additionally, between 4.0 Ma and 3.5 Ma, there was either no change in diversity or an increase in diversity for all families, with the exception of the Cancellaridae. This could also be due to the sample bias during the 4.5 Ma to 4.0 Ma interval (TB5).

Community Stasis

The Neogene of the Cibao Valley Basin is an ideal system for exploring the relationship between habitat change and associated biotic responses over geological timescales. The results of this study show faunal instability in the presence of environmental changes over time. The Jaccard similarity coefficient showed that species similarities within families and between most of the study formations are significantly lower than 1, indicating faunal instability within this study system (Fig. 8).

The cluster analysis in Figure 9 shows a separation between two types of paleoenvironments in this study area; Cluster 1 (6.5 Ma - 5.0 Ma) represents a shallow-water environment and Cluster 2 (5.0 Ma - 3.5 Ma) represents a deep-water environment. Cluster 2, however, represents a link between a shallow-water environment and a deep-water environment due to shallow-water species being present in a deeper water environment. According to Budd *et al.* (1999), Faviidae species have been found in slump deposits in deeper water deposits (i.e., were transported from shallower habitats). Additionally, Vokes (1989a) found evidence for gravity-flows in five localities (TU 1352, 1366, 1413, NMB 15832, 15833) in this study area. Within these five localities, five shallow-water species (*Chicoreus cornurectus*, *Corbula (Caryocorbula) sericea*, *Lyria (Lyria) pulchella*, *Morum (Oniscidia) domingense*, and *Murex messorius*) were part of RG1. The presence of some shallow-water species in the deep-water environments suggests that these species were transported to deeper waters after death. The cluster analysis in Figure 10 represents two different clusters where mollusks tend to group together in Cluster 1 and corals tend to group together in Cluster 2. These taxa could be separating into these clusters based on the paleoenvironmental settings in which they existed.

The DCA in Figure 11 illustrated species distribution across time through the changing habitats. Axis 1 of the DCA represented the scores of the species while Axis 2 represented the scores of the time interval for each river (RC1-RC6 and RG1-RG6). The results show a larger number of species in intermediate-water environments, while there are fewer species recorded in the deeper water depths for both mollusk and coral species (Fig. 11). These results also indicate the presence of shallow-water species in deep-water environments, which is consistent with the results from the R-mode cluster analysis.

The results of the present study indicated that the mollusk and coral assemblages favor shallow- to intermediate-water depths rather than deeper water conditions, which is consistent with Anderson's (1994) research that showed a higher number of corbulid species during the Miocene (shallow- to intermediate-water depths) than in the Pliocene (deep-water depths). The results of this study also revealed that only 14% of the 179 species persisted from the late Miocene Cercado Fm. into the middle Pliocene Mao Fm., and from shallow- into deep-water environments. Similar results are found in research conducted by Rivera *et al.* (2008), which showed only 21 of more than 300 mollusk species (<7%) persisted from the Cercado Fm. to the Gurabo Fm. in the Cibao Valley Basin. Furthermore, research by Klaus *et al.* (2008) on 104 coral species indicated faunal instability through the Cercado, Gurabo, and Mao formations. The results from this study are consistent with those of previous authors: a low percentage of species persist through time across the different paleoenvironmental settings, indicating faunal instability in the Cibao Valley Basin.

In a broader context, Cenozoic tropical American coral-reef faunas have been thoroughly studied by Budd (2000). Her results revealed three major extinction periods (Middle–Late Eocene, Late Oligocene–Early Miocene, and Plio–Pleistocene) of coral-reef faunas that correlate with large-scale environmental changes. Additionally, the total number of species increased during intervals of high reef development (Middle–Late Eocene, Late Oligocene–Earliest Miocene, and Late Miocene–Late Pliocene). Budd (2000) also noted that the species composition from the Late Miocene to the Early Pliocene (8 to 4 Ma) more-or-less remained the same, and new species were added to communities during the Plio-Pleistocene. The results of Budd's (2000) analysis on Caribbean coral-reef faunas, which indicated no major decline in species composition through time across different paleoenvironmental settings, are at odds with the results of the present study because there was evidence for a decline in species composition.

A notable example of faunal stability comes from an analysis of invertebrate marine species collected from the Devonian Hamilton Group in the Appalachian Basin of New York State (Brett *et al.* 2007). The Hamilton Group is an ideal location for an analysis of faunal stability due to the diverse, well-preserved fauna, and the paleoenvironmental changes that occurred in the study system over a long period of time (Brett *et al.* 2007). The results of this study revealed that when an analysis of faunal stability was conducted on a narrow geographic scale, faunal instability was apparent in the study system. On the other hand, when the depositional environment of the basin was analyzed as a whole, the results indicated faunal stability within this system. In light of the work by Brett *et al.* (2007), further research should be conducted on faunal stability throughout the Cibao Valley Basin beyond the two river valleys considered here. Such future research could reveal whether faunal stability occurs throughout the basin or only in sections of the basin. Considering that abundance data were not available, additional research should also be conducted on the species diversity and paleoecology of this study system. Many of the invertebrate taxa from the Dominican Republic have remained unstudied, and thus the full scope of biodiversity patterns in this system will remain unknown without additional diversity data.

CONCLUSION

Using a newly developed database of marine invertebrate species from the Neogene of the Dominican Republic, species-level diversity trends and the community structure of 16 families of bivalves, gastropods, and corals were analyzed. The diversity patterns of the coral and mollusk species may appear to have fluctuated during this time period due to a sampling bias in TB5 (5.0-4.5 Ma). The R-mode cluster analysis indicated two clusters, one representing shallow- to deep- water environments and the other indicating very deep-water environments. The Q-mode cluster analysis also indicated two clusters, one including almost all mollusk species and the other including mostly coral species. The mollusks and corals were also found to have a low similarity of species from the Cercado Fm. to the Mao Fm. in the Cibao Valley Basin, with only 14% of species persisting across this 3 Myr span. In addition, the species richness was higher in the intermediate-water depths and lower in the very deep-water depths. In all, the results of this study indicate an unstable community of species that fluctuated with the paleoenvironmental changes that occurred during the 3My time span in this study system.

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