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Biogeographic Regionalization and Transition Zones

Combining Historical and Ecological Methods Provides New Insights for the Recognition of Biogeographical Areas and Their Relationships: The Case of the Gulf of Mexico

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ABSTRACT

Aim: Biogeographical regionalisation is an evolutionary system of nested areas representing the geographic organisation of life on the planet, which is fundamental for understanding basic and applied aspects related to the ecology, evolution and conservation of biotas and their habitats. The conceptual and practical development of biogeographical regionalisation has been diverse, deriving from two main subdisciplines: historical or evolutionary biogeography and ecological biogeography. This division has prevented the consolidation of an integrative discipline, hampering its advancement. In this work, we implement a new methodology for conducting biogeographical regionalisation by integrating two traditional techniques coming from historical and ecological biogeographical studies: parsimony analysis of endemism and hierarchical clustering analysis into a coherent methodological framework (PAE-HCA).

Location: Gulf of Mexico, Western Atlantic.

Taxon: Multi-taxa.

Methods: The framework consists of three main steps: (1) identifying areas of distributional congruence, (2) establishing a spatial structure of the areas recognised and (3) recognising area relationships. The method includes the establishment of biogeographic hypotheses that can be tested statistically regarding the membership of the units that conform to each area and their affinity, providing robustness and biogeographic assertion. This methodological framework was tested with a comprehensive occurrence database from the Gulf of Mexico and adjacent waters.

Results: A total of 126 areas of distributional congruence were recovered, which were grouped into three main biogeographic areas with strong statistical support. These areas are congruent with geological and oceanographic features of the region, supporting the hypothesis that the Gulf can be divided into two main components, one characterised by neritic waters and the other characterised by oceanic waters.

Main Conclusions: The present study constitutes the first attempt to integrate historical and ecological techniques into a robust methodological framework. Future perspectives include implementing this approach in different environments, such as terrestrial, considering different geographic scales, including global studies, or different taxa.

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1 | Introduction

Biogeography has been historically approached from ecological or historical/evolutionary perspectives, each advocating for its original epistemological ideas, methodologies and concepts (Posadas et al. 2006; Crisci et al. 2006; Morrone 2007; Ricklefs and Jenkins 2011; Ebach and Parenti 2015). Some authors consider this division conventional (Morrone 2007); however, each approach has developed robust and independent methodologies, leading to their consolidation as independent disciplines (e.g., MacArthur and Wilson 1963; Nelson and Platnick 1981; Morrone and Crisci 1995; Kreft and Jetz 2010). Ecological biogeography focuses on 'proximal causes', i.e., it seeks causal explanations for the distribution of taxa in the present time, as an immediate response to environmental variability (Posadas et al. 2006; Monge-Nájera 2008; Ricklefs and Jenkins 2011). Historical biogeography, in contrast, argues for 'ultimate causes', seeking evolutionary explanations of the taxa distribution over the geological timescale, resulting from geological, speciation/extinction, vicariance and dispersal processes (Nelson and Platnick 1981; Morrone and Crisci 1995; Humphries and Parenti 1999; Crisci 2001; Morrone 2007). This division has limited the progress of biogeographical regionalisation (BR), a cornerstone in biogeography, due to the implementation of conceptually and operationally different methods, as well as the incompatibility in the definition of basic biogeographic units such as ecoregions, areas of endemism, or bioregions.

Regardless of the variety of approaches, BR has historically aimed to delimit geographical areas based on endemic taxa (Morrone 2018), which is crucial for two main reasons. First, it provides insights into the evolutionary history of both the areas and the biotas inhabiting those areas. Second, it enables the delimitation and description of geographical areas in terms of their biodiversity, being crucial to conservation management plans (Whittaker et al. 2005; Costello et al. 2017). For this reason, BR has drawn the attention of many scientists from diverse disciplines such as ecology, geography, systematics and palaeontology, among others (Ebach 2015). The multidisciplinary nature of biogeography, reflected in BR, has caused many debates throughout history, preventing a unification of concepts, ideas, methods and approaches, and hampering an efficient communication among biogeographers (Morrone 2018). Methodologically, the lack of integration is more evident. For instance, ecological BR aims to recognise ecoregions/bioregions upon hierarchical, non-hierarchical, or network algorithms, most of them based on the estimation of beta diversity, not necessarily reflecting a natural area system (natural = monophyletic) (Kreft and Jetz 2010; Legendre 2014; Denelle et al. 2025). In contrast, historical BR aims to recognise a system of natural areas that are hierarchically organised into realms, regions, dominions, provinces and districts (Ebach et al. 2008), based on the identification of areas of endemism or generalised tracks (Morrone 1994; Szumik et al. 2002).

The integration of ecological and historical approaches is often highlighted as desirable in the literature (Posadas et al. 2006; Morrone 2009; Sanmartín 2012); however, attempts at a methodological level are scarce. Some studies have applied ecological and historical techniques within their aims, searching for congruent results from philosophically, conceptually and

operationally different methods, but have lacked a coherent integration as a logical sequence of steps (e.g., Fattorini 2022; Ahuatzin-Hernández et al. 2023). On the other hand, the combination of ecological and historical techniques has been proposed as a methodological solution to select the most reliable areas of endemism recovered with optimality criterion (i.e., sensitivity analysis = NDM/VMDM + clustering techniques), but this proposal lacks an integrative narrative explaining the advantages of combining both groups of techniques, while its results are not usually interpreted with historical implications (Hoffmeister and Ferrari 2016; Ferrari et al. 2022; Alvares et al. 2022; Ribeiro Machado et al. 2024).

In this work, we explore the combination of two classical techniques, i.e., parsimony analysis of endemism (PAE) and hierarchical cluster analysis, usually implemented in historical and ecological biogeographic studies, into a coherent methodological framework (PAE-HCA). This provides an alternative and integrative approach to conducting biogeographical regionalisation, discussing the advantages of both techniques. For this aim, we analysed a multi-taxa dataset from the Gulf of Mexico and adjacent waters, a region with a well-documented geological and oceanographic history, which has motivated several biogeographic works in recent years (e.g., Engle and Summers 2000; Vilchis et al. 2018; Paz-Ríos et al. 2021; Ahuatzin-Hernández et al. 2023, 2024; Hernández-Zaltrón et al. 2025). Although there have been attempts to regionalise the Gulf of Mexico on different approaches (e.g., Spalding et al. 2007; Wilkinson et al. 2009), there is currently no integrative vision of the biogeography of this region. This fact, together with its geographical location, in which warm-temperate and tropical water converge (Neigel 2009), makes the Gulf of Mexico an area of particular interest for biogeographical studies.

2 | Methods

2.1 | Dataset and Preparation Process

The data implemented in this study consisted of a comprehensive multi-taxa dataset built with occurrence information from previous studies in the Gulf of Mexico and adjacent waters (Pérez-Botello and Simões 2021; Chávez-López 2022; Vital et al. 2023; Sanvicente-Añorve et al. 2023; Ahuatzin-Hernández et al. 2023, 2024; Cuadrado et al. 2024; Hernández-Zaltrón et al. 2025; Gómez-Mendicuti et al. 2025). This information consists of records obtained from peer-reviewed literature, as well as sampling or museum-revised specimens and taxonomically and geographically curated records from the Global Biodiversity Information Facility (GBIF) and the Ocean Biodiversity Information System (OBIS) databases. Additionally, this information was supplemented with databases retrieved from GBIF, i.e., Ugalde et al. (2021), Wolff et al. (2023), Muciño-Reyes et al. (2024), Escobar Briones (2025) and Chávez Ortiz (2025). After merging the information, duplicate records were flagged and removed using the 'CoordinateCleaner' package (Zizka et al. 2019). The accuracy of the dataset was verified manually by cross-checking each record with the World Register of Marine Species (WoRMS), correcting synonyms and typos and removing invalid taxa and those falling out of the distributional range maps provided by this platform (WoRMS). The final dataset accounted for 78,689

records from 2937 taxa (Data S1) (Figure 1). The information was then coded into a community matrix with species in the columns and operational geographic units (OGUs) in the rows ($n=215$). OGUs represent quadrants of $1^{\circ} \times 1^{\circ}$.

2.2 | Parsimony Analysis of Endemicity With Hierarchical Clustering Analysis (PAE-HCA)

The methodological framework proposed in this study consists of three main steps, which are described below (Figure 2). The first paragraph of each subsection details the theoretical framework and how to carry out each step in theory. The second paragraph describes the methods implemented in the case study of the Gulf of Mexico.

2.2.1 | Identification of Areas of Distributional Congruence

There are different methods to recognise areas of distributional congruence; however, areas of endemism are the best representatives of this concept, being fundamental units in historical biogeographical studies (Morrone 1994, 2001; Crother and Murray 2011; Aagesen et al. 2013). In this sense, PAE has been one of the most widely used methods for identifying areas of endemism from the

late 80s to the present. PAE constructs cladograms based on the cladistic analysis of presence-absence matrices of species and supraspecific taxa, allowing hypotheses to be formulated regarding biotic components and their relationships (Morrone 2014). In PAE-HCA, PAE is proposed to discriminate areas with congruent distributional patterns from those lacking such patterns, which usually obscure biogeographical analyses due to the presence of taxa with wide or random distributional ranges. Because of the nature of PAE, areas of endemism can be considered hypotheses of primary biogeographic homology, resulting from a common biogeographic history of the taxa occurring in them; thus, retaining their historical component.

To conduct the PAE, a hypothetical area coded with 0s was added to the community matrix in order to root the resulting cladogram(s). The matrix was then analysed in TNT 1.6. (Goloboff and Morales 2023) (Data S2). Implied weights with default value ($k=3$) were used, as well as the New Technology Search algorithm and Ratchet as the search strategy. The remaining options were left at their default settings. To recover as many areas of endemism as possible, autapomorphic taxa were preserved. Areas of endemism were identified as those clades supported by at least two synapomorphic taxa. Clades including different OGUs and supported by at least two synapomorphies were considered to represent higher-level areas of endemism.

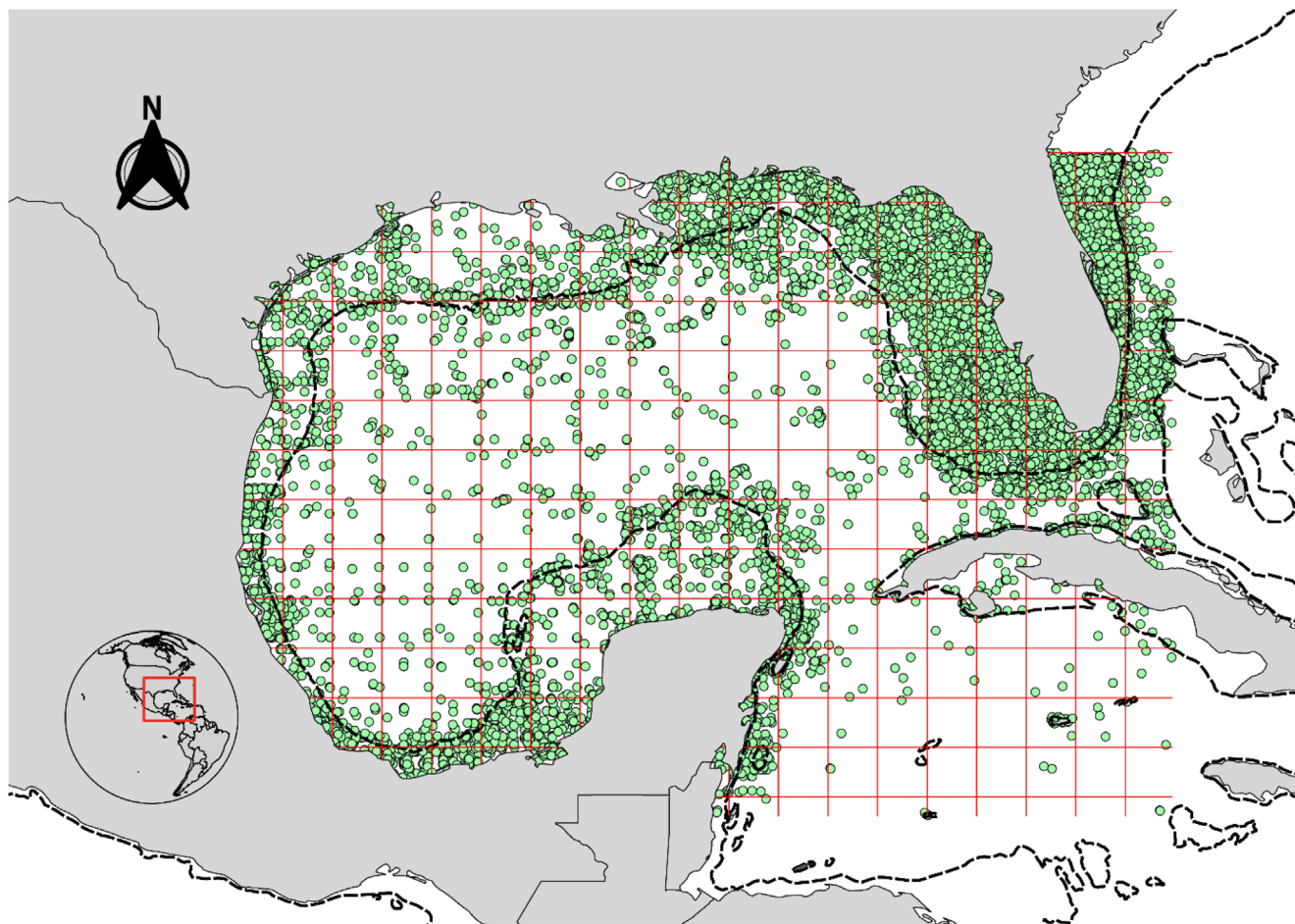


FIGURE 1 | Occurrence records superimposed in the OGUs grid of $1^{\circ} \times 1^{\circ}$. The dashed line indicates the 200 m isobath, representing the continental shelf.

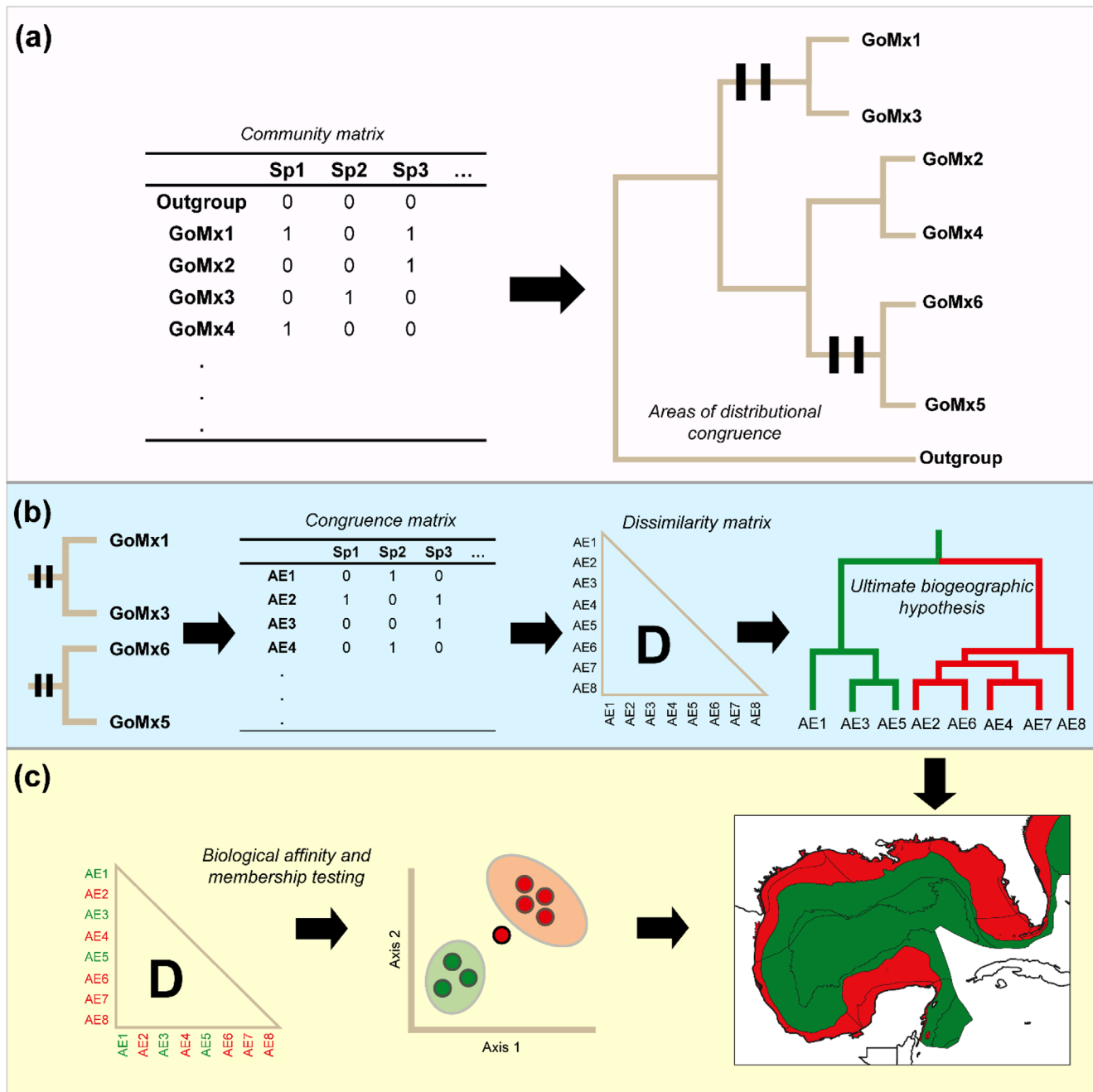


FIGURE 2 | Workflow to conduct step by step the parsimony analysis of endemism with hierarchical clustering analysis (PAE-HCA). (a) Identification of areas of distributional congruence. (b) Recognition of ultimate biogeographic hypothesis. (c) Testing area relationships and membership.

2.2.2 | Recognising Ultimate Biogeographic Hypothesis

Once the areas of distributional congruence were recovered, they must be recoded into a new matrix, composed exclusively of areas of endemism (congruence matrix). Since some of the original taxa do not occur in the congruence matrix, they must be removed, and it must be verified that all OGU contain at least one taxon. Hierarchical clustering is then applied to the congruence matrix. It is worth mentioning that implementing a hierarchical method is fundamental to obtaining a biogeographical regionalisation—a scheme of hierarchically organised geographic areas—. This means that, when analysing different

levels of the tree, new nested areas can be recovered from the major levels. This step aims to identify a spatial structure in historical units by recognising relationships among areas based on their shared species. Since the resulting topology is recovered from individual biogeographic hypotheses (areas of endemism), the consensus tree can be interpreted as an ultimate biogeographic hypothesis, which can be statistically tested using bootstrap resampling.

To conduct this step, beta diversity was estimated from the congruence matrix (Data S3), implementing the *beta.pair* function of the 'betapart' package (Baselga and Orme 2012), and using

the Jaccard index to partition beta diversity into turnover and nestedness components. A hierarchical tree was then built from the turnover dissimilarity matrix using the *hclust_hierarclust* function of the 'bioregion' package (Denelle et al. 2025). This function considers that the order of sites in the distance matrix can influence the topology of the tree, so consensus clustering, including consensus tree topology, is calculated by reconstructing the tree from top to bottom by iteratively identifying the majority decision binary split among many randomisations (Denelle et al. 2025). The unweighted pair-group method using arithmetic averages (UPGMA) was chosen, with 100 trials of randomisation and the iterative consensus tree option. Based on the consensus tree topology, two cut-off dissimilarity levels were analysed ($k=2$ and $k=3$). The uncertainty of the biogeographical areas was assessed with the 'pvclust' package using 10,000 bootstrap replications (Suzuki and Shimodaira 2006). We passed the turnover matrix estimated with the Jaccard index to the pvclust analysis. As the 'bioregion' package implements consensus clustering, the resulting tree topology was not identical to that of the pvclust analysis. Nevertheless, the three biogeographical areas of the ultimate biogeographic hypothesis were recovered and tested. In order to compare the results of PAE-HCA with a classical clustering, a hierarchical clustering was additionally conducted on the original community matrix (step 1), considering the same criteria and packages implemented to the recognition of the ultimate biogeographic hypothesis (Data S4).

2.2.3 | Testing Area Relationships and Membership

Once the biogeographical areas have been identified, the dissimilarity matrix estimated in step two can be subjected to an ordination analysis, associating each OGU with the biogeographic area to which it was previously assigned in the hierarchical clustering analysis. This step looks for recognising biotic affinities among biogeographical areas. Ordination analyses are useful because they allow us to evaluate biotic components into a spatial gradient, which is crucial in the recognition of geographical boundaries and transition zones (Kreft and Jetz 2010). If applicable, the membership of each OGU to each biogeographical area can be statistically tested using confidence ellipses.

We performed a principal coordinates analysis (PCoA) on the dissimilarity matrix implemented in step two, using the *pcoa* function of the 'ape' package (Paradis and Schliep 2019), and associating with colours the membership of each OGU to its respective biogeographic area. The *betadisper* function of the 'vegan' package was used to estimate confidence ellipses at the 0.95% confidence level. This was achieved through an analysis of the multivariate homogeneity of the group's dispersions between the OGUs and the centroids of each group (biogeographical area) (see Anderson 2006; Anderson et al. 2006).

3 | Results

3.1 | Areas of Distributional Congruence

PAE retained one area cladogram with a consistency index of 0.179 and a retention index of 0.471. This cladogram recovered 24 areas of higher-level endemism comprising 126 OGUs

(Figure 3a), which are found in shelf, escarpment and oceanic zones. Most of these areas of endemism were aggregated around the Yucatán and Florida peninsulas, as well as in the Sigsbee escarpment (Figure 3b).

3.2 | Ultimate Biogeographic Hypothesis

The consensus tree resulting from the hierarchical clustering of areas of endemism had a cophenetic correlation coefficient of 0.881. At a cut height of 0.937, the consensus tree topology allowed for hypothesising on the existence of two main biogeographical areas: 'Neritican' and 'Sigsbeean' (Figure 4a). The Neritican area encompasses the entire continental shelf of the Gulf of Mexico, whereas the Sigsbeean area is confined to the northern Gulf, mainly in the Sigsbee escarpment (Figure 4b). Both areas harbour distinctive biotas that show no affinity with each other (Figure 4c). At a cut height of 0.875, the Neritican area splits, originating the 'Loopean' area (Figure 4a), which has a discontinuous distribution, characterising part of the Yucatán channel, the northern part of the Yucatán Peninsula, and the Florida Straits (Figure 4b). The Loopean area's biota showed a closer biotic affinity with the Neritican area than the Sigsbeean (Figure 4c). Multiscale bootstrap resampling provided high levels of confidence for the three areas: Neritican = 90, Sigsbeean = 85 and Loopean = 91 (Figure 4a).

4 | Discussion

4.1 | Biogeography of the Gulf of Mexico

The Neritican area supports the main biogeographic division of the Gulf of Mexico into two areas, one characterised by neritic waters, represented by the continental shelf and its associated environments, and the other characterised by oceanic waters, contrasting with traditional schemes that classified the Gulf into northern and southern components (e.g., Spalding et al. 2007; Wilkinson et al. 2009). This idea has been pointed out previously, indicating the continental slope as a boundary between both areas (Toonen et al. 2016; Ahuatzin-Hernández et al. 2023; Oliveira et al. 2024; Hernández-Zaltrón et al. 2025). This becomes more relevant when considering differences among neritic and oceanic areas. Neritic environments, for example, are characterised by diverse habitats, such as river deltas, estuaries, lagoons, reefs, or bays, as well as high productivity, resulting in high biodiversity and endemism (Toonen et al. 2016; Fujiwara and Kon 2020). On the other hand, oceanic environments tend to be more homogeneous and sometimes oblivious to coastal phenomena, having a more complex vertical stratification, with deep areas lacking sunlight, low temperature and high hydrostatic pressure (Fujiwara and Kon 2020).

Biologically, the differences between neritic and oceanic biotas are also evident in light of the evolutionary context. For instance, the development of some hydrozoans, in either neritic or oceanic environments, has shaped their evolutionary history, as reflected in their life cycle, which typically includes a benthic polyp and a planktonic medusa. Neritic hydrozoans, for example, possess complex and well-developed polyp forms

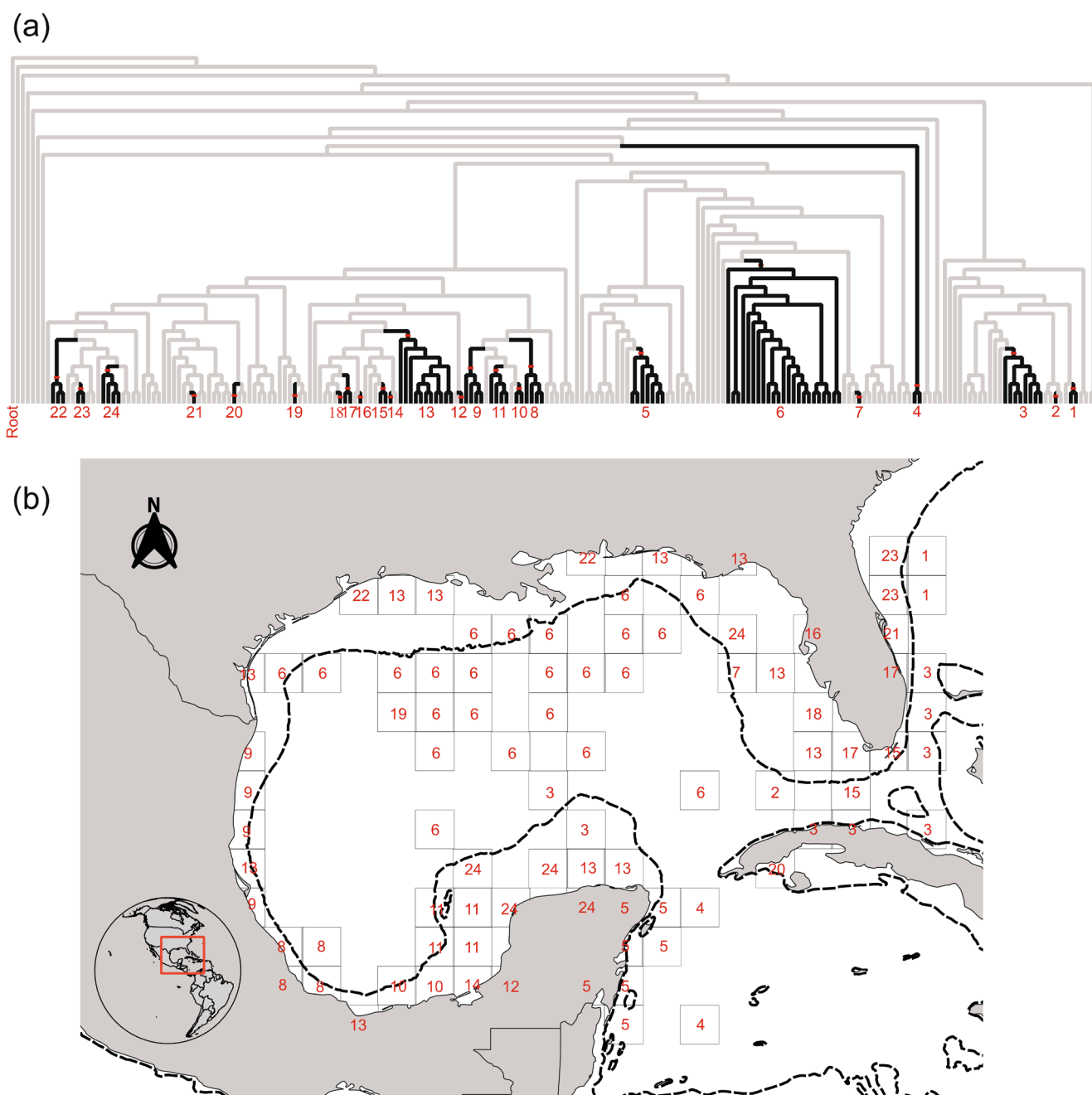


FIGURE 3 | Areas of distributional congruence. (a) Cladogram resulting from the parsimony analysis of endemism. Transversal red bars, bold branches and numbers represent areas of endemism (clades supported by at least two synapomorphic taxa). (b) Geographical location of the areas of endemism. Numbers correspond with (a). The dashed line indicates the 200m isobath, representing the continental shelf.

in their life cycle, even losing the medusa stage in some cases as an adaptation to living in environments with a great variety of substrates (Boero et al. 1992, Cartwright et al. 2021). Conversely, hydrozoans inhabiting the open ocean exhibit the opposite pattern, as the planktonic medusa becomes the dominant form, lacking a polyp stage, due to living in environments with scarce substrate availability for fixation (Bentlage et al. 2018). Examples of adaptation to open ocean in polychaetes include avoidance behaviours when developing in deep-sea brine pools, symbiotic relationships with autotrophic bacteria in deep-sea vents and cold seeps, and the development of motile structures for active swimming in some members of the subclass Errantia (Glasby et al. 2021).

Fish are no exception. For instance, the development of unlit colours by the sun, and the presence of big eyes in the mesopelagic zone—which tend to become small or vestigial in deeper areas—are adaptations for living in different strata of the open ocean. These adaptations become even more evident when considering the vertical gradient, as seen in the loss of swim bladders, which contrasts with the physiological and morphological characteristics of neritic fish (Haedrich 1996). Together with the recognition of the Neritican area, this evidence supports the hypothesis that the Gulf of Mexico can be divided into two main biogeographical components, neritic and oceanic (despite this study only recovered the neritic component), instead of north and south.

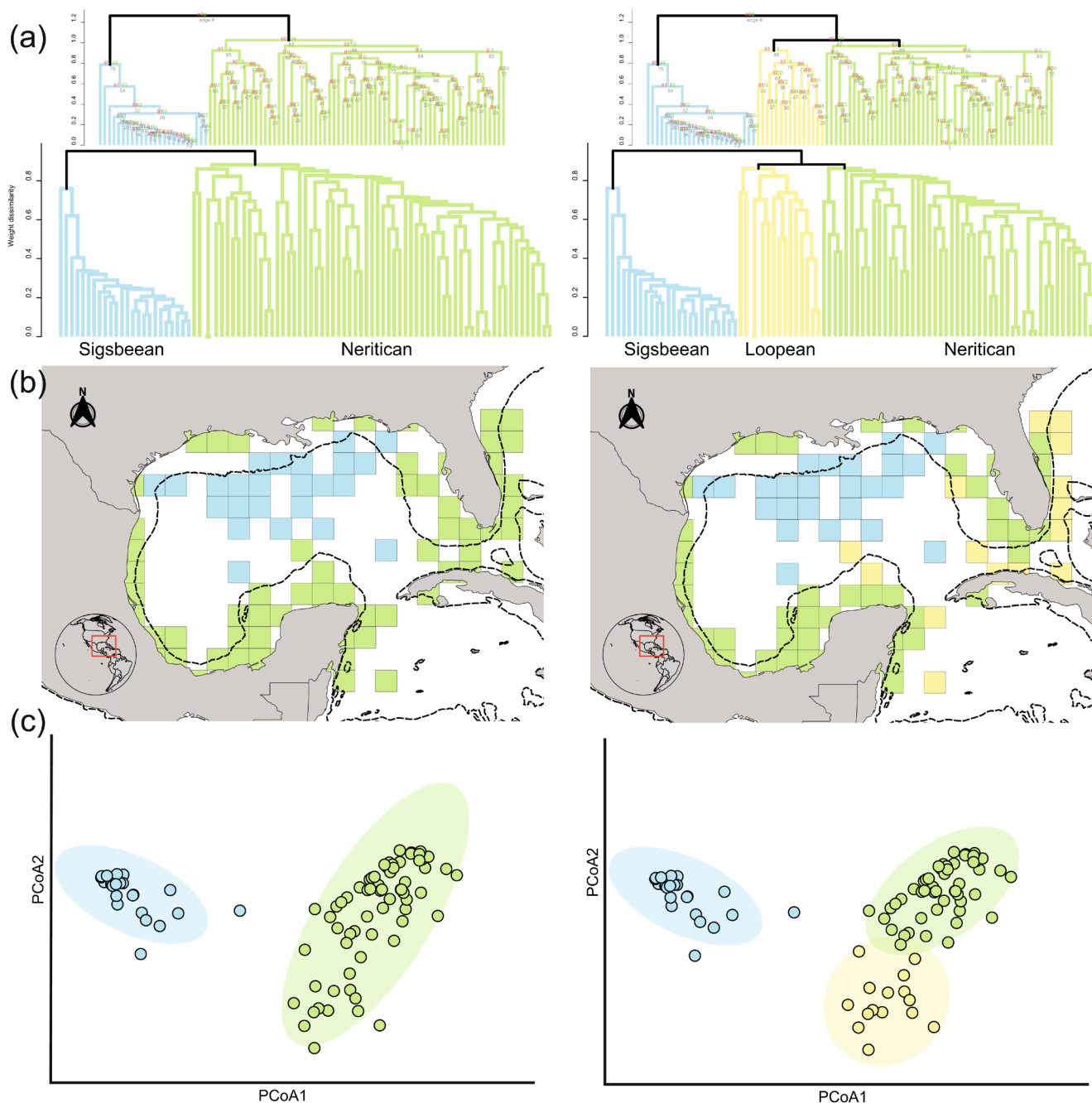


FIGURE 4 | Biogeographical areas of the Gulf of Mexico and adjacent waters. (a) Consensus tree at two different cut-off levels, representing an ultimate biogeographic hypothesis. The smaller trees over each consensus tree indicate the supporting values for the biogeographical areas after the pvcust analysis. (b) Geographic location of the biogeographical areas. The dashed line indicates the 200 m isobath, representing the continental shelf. (c) Principal coordinates analysis (PCoA) on the dissimilarity matrix used to identify the biogeographical areas. Ellipses represent confidence ellipses at the 0.95% confidence level.

The Sigsbee area is consistent with previous regionalisation conducted with foraminifera and echinoderms (Culver and Buzas 1981; Hernández-Zaltrón et al. 2025), thereby supporting its establishment as a biogeographical area. The Sigsbee area is characterised by high relief and ridges, as well as the influence of the Mississippi River plume, which provides the area with organically enriched soft sediments (Shih et al. 1977, Buffler and Worzel 1978, Williams et al. 2011, Yarbuh and Contreras 2017). These characteristics, together with the sharp change in bathymetry, have historically shaped a unique biota adapted to

living in a transitional environment between shallow and deep waters (Wei et al. 2010; Hernández-Zaltrón et al. 2025), explaining its distinct biological composition that shows no affinity with the other biotic components.

The discontinuous distribution of the Loopean area may otherwise reflect two important aspects: the dispersal process caused by the Loop Current, given that its route partially matches the distribution of the Loopean area, and the historical and ecological connection suggested between the Yucatán and Florida

peninsulas (Vilchis et al. 2018; Paz-Ríos et al. 2021; Ahuatzin-Hernández et al. 2023). It has historically been hypothesised that the Yucatán and Florida blocks were connected (~140–160 Mya), due to the superposition of the Yucatán block with that of Florida, before its counterclockwise rotation and establishment in its current location (see Bird et al. 2011). Ecologically, both the Florida and Yucatán shelves share similar features, as they are extensive tropical areas with karst characteristics and extensive shallow waters, where similar ecosystems exist, such as lagoons, bays, coral reefs and mangrove forests, among others (Spalding et al. 2007; Wilkinson et al. 2009). Therefore, finding similar biological composition or affinities between these two areas is not surprising.

4.2 | Parsimony Analysis of Endemicity With Hierarchical Clustering Analysis (PAE-HCA)

PAE-HCA proved to be efficient for recovering biogeographical areas previously proposed, congruent with the geological, physiographic and oceanographic features of the region (e.g., Culver and Buzas 1981; Ahuatzin-Hernández et al. 2023; Hernández-Zaltrón et al. 2025). Moreover, its performance was superior to that of the classical clustering analysis conducted on the original community matrix, which had a cophenetic correlation coefficient of 0.644. This performance is reflected in the consensus tree, which was unable to classify successfully some branches (see Data S4). Classical clustering recovered four areas, some of which were recognised in previous studies (e.g., Ahuatzin-Hernández et al. 2023); however, PAE-HCA resulted in a clearer, more easily interpretable hypothesis, as shown above. This differentiation occurs because PAE-HCA removes OGU's lacking distributional patterns, resulting in a finer result. Furthermore, the historical background of PAE facilitates its interpretation in an evolutionary context. We proposed PAE for recognising areas of distributional congruence (areas of endemism) as it considers the restriction and overlap of endemic taxa (sympatry), which is fundamental to raising hypotheses of a common biogeographic history (Morrone 2014; Escalante 2015). In biogeography, endemism is a cornerstone, as it allows the recognition of geographic areas based on the endemic taxa inhabiting them. Hence, endemism must be considered in any regionalisation attempt. Despite different interpretations of endemism, a taxon cannot be endemic to more than one area at a given scale, nor can it represent degrees of endemism. Thus, a taxon is either endemic to an established region, or it is not (Escalante 2015; Morales-Guerrero et al. 2017). In this sense, PAE meets these criteria.

Unlike traditional systematic cladograms, which represent a phylogenetic hypothesis regarding the evolutionary relationships among the analysed taxa, an area cladogram recovered with PAE fails to recognise reliable area relationships among the OGU's under study. This is because PAE can group areas based on shared absences, and we lack knowledge on the circumstances under which the areas and taxa evolved (Brooks and van Veller 2003; Nihei 2006; Escalante 2011). Areas of endemism are often the only informative units of the area cladogram and are interpreted as individual hypotheses of primary biogeographic homology. Therefore, implementing hierarchical clustering to areas of distributional congruence obtained with PAE enhances the interpretation and analysis of the relationships

among these areas. We recommend using the beta diversity turnover component for finding ultimate biogeographic hypotheses, as it is least affected by the variation in richness (i.e., it is richness-independent) and does not consider double absences as a (dis)similarity criterion. This is important because variation in richness is biased in large online databases, due to unequal sampling effort (Baselga 2010; Kreft and Jetz 2010). Likewise, the UPGMA has proved to be the best algorithm to recognise clusters (Kreft and Jetz 2010; Denelle et al. 2025), which is consistent with the cophenetic correlation coefficient, and the consensus tree topology obtained in this study. This performance was corroborated by the PCoA, which displayed two and three well-defined and mutually exclusive groups at two different cut-off levels, respectively, with a high degree of membership in the OGU's that conform to each group.

Different techniques have been proposed for conducting biogeographical regionalisations (Morrone 2018). Frameworks based on multivariate techniques have demonstrated good results (e.g., Kreft and Jetz 2010; Vilhena and Antonelli 2015; Daru et al. 2020), although they lack the endemism component. For instance, cluster and network analyses rely on the estimation of (dis)similarity matrices (representing percentages of shared species), yet species are lost when conducting pairwise comparisons (Legendre 2014; Denelle et al. 2025), preventing the faithful estimation of endemic taxa. On the other hand, classic biogeographical methods, such as PAE, are among the most implemented techniques for recognising natural area systems. Nevertheless, PAE has some limitations. For example, it may group areas based on shared absences, and it lacks a direct statistical test to falsify hypotheses it raised. In this sense, PAE-HCA overcomes these limitations by integrating the strengths of both approaches. It uses PAE to discriminate areas with distributional noise and retain areas with distributional congruence. It then implements clustering to determine the spatial structure and area relationships of the PAE results, resulting in an ultimate biogeographic hypothesis that can be tested statistically in a direct manner.

PAE-HCA may look similar to the sensitivity analysis proposed by Hoffmeister and Ferrari (2016); however, both methodologies are different. Sensitivity analysis explores the results of different analyses, considering different criteria and parameters, whereas PAE-HCA is not a multi-criteria method. It represents an improvement in the statistical interpretation of biogeographic hypotheses. Furthermore, PAE-HCA strictly considers the concept of endemism by recovering sympatry patterns, which are then subjected to multivariate analyses. In contrast, the sensitivity analysis fails to identify strict sympatry patterns due to its index nature (Escalante 2015). The sensitivity analysis aims to identify areas of endemism, whereas in PAE-HCA, identifying areas of endemism is only one step of the framework, to later analyse those areas with clustering methods, acquiring a new meaning that can be interpreted as an ultimate biogeographic hypothesis that is the object of statistical testing.

Finally, PAE-HCA is not a variant of PAE but rather a new framework that uses PAE as a step to recognise distributional congruence areas. This becomes evident when comparing the results and hypotheses obtained solely with PAE or classical clustering (Data S4) with those obtained with PAE-HCA. The main flaw

of the method is that it depends on recovering a representative number of areas of endemism of the study area. For this, large datasets, considering different taxa, are usually needed. Therefore, it is expected that future improvements to PAE-HCA will involve its implementation at different geographic scales, considering different taxonomic groups and environments.

Author Contributions

Conceptualisation: J.M.A.-H., V.M.V.-M. Formal analysis: J.M.A.-H. Supervision: J.J.M., V.M.V.-M., A.J.S. Writing – original draft/review and editing: J.M.A.-H., J.J.M., A.J.S. All the authors read and approved the final draft of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data supporting the findings of this study are available within the paper and its [Supporting Information](#).

References

- Aagesen, L., C. Szumik, and P. Goloboff. 2013. "Consensus in the Search for Areas of Endemism." *Journal of Biogeography* 40: 2011–2016. <https://doi.org/10.1111/jbi.12172>.
- Ahuatzin-Hernández, J. M., J. J. Morrone, and V. M. Vidal-Martínez. 2023. "Biogeographic Patterns of Hydrozoans in the Gulf of Mexico and Adjacent Waters: Biological Assemblages, Beta Diversity, and Endemism." *Marine Ecology Progress Series* 720: 85–94. <https://doi.org/10.3354/meps14407>.
- Ahuatzin-Hernández, J. M., J. J. Morrone, and V. M. Vidal-Martínez. 2024. "Biotic Assemblages of Gelatinous Zooplankton in the Gulf of Mexico and Adjacent Waters: An Evolutionary Biogeographic Approach." *PLoS One* 19: e0307933. <https://doi.org/10.1371/journal.pone.0307933>.
- Alvares, D. J., A. Ferrari, and M. Borges-Martins. 2022. "Geographic Distribution Patterns of Amphibians and Reptiles From the Uruguayan Savanna." *Systematics and Biodiversity* 20: 1–17. <https://doi.org/10.1080/14772000.2022.2039796>.
- Anderson, M. J. 2006. "Distance-Based Tests for Homogeneity of Multivariate Dispersions." *Biometrics* 62: 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>.
- Anderson, M. J., K. E. Ellingsen, and B. H. McCaule. 2006. "Multivariate Dispersion as a Measure of Beta Diversity." *Ecology Letters* 9: 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>.
- Baselga, A. 2010. "Partitioning the Turnover and Nestedness Components of Beta Diversity." *Global Ecology and Biogeography* 19: 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>.
- Baselga, A., and C. D. L. Orme. 2012. "Betapart: An R Package for the Study of Beta Diversity." *Methods in Ecology and Evolution* 3: 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>.
- Bentlage, B., K. J. Osborn, D. J. Lindsay, R. R. Hopcroft, K. A. Raskoff, and A. G. Collins. 2018. "Loss of Metagenesis and Evolution of a Parasitic Life Style in a Group of Open-Ocean Jellyfish." *Molecular Phylogenetics and Evolution* 124: 50–59. <https://doi.org/10.1016/j.ympev.2018.02.030>.
- Bird, D. E., K. Burke, S. A. Hall, et al. 2011. "Tectonic Evolution of the Gulf of Mexico Basin." In *Gulf of Mexico: Origin, Waters, and Biota, Vol 3: Geology*, edited by N. A. Buster and C. W. Holmes, 3–16. Texas A&M University Press.
- Boero, F., J. Bouillon, and S. Piraino. 1992. "On the Origins and Evolution of Hydromedusan Life Cycles (Cnidaria, Hydrozoa)." In *Sex Origin and Evolution. Selected Symposia and Monographs UZI*, edited by R. Dallai, vol. 6, 59–68. Mucchi, Modena.
- Brooks, D. R., and M. G. van Veller. 2003. "Critique of Parsimony Analysis of Endemism as a Method of Historical Biogeography." *Journal of Biogeography* 30: 819–825. <https://doi.org/10.1046/j.1365-2699.2003.00848.x>.
- Buffler, R. T., and J. L. Worzel. 1978. "Deformation and Origin of the Sigsbee Scarp—Lower Continental Slope, Northern Gulf of Mexico." In *10th Annual Offshore Technology Conference*, vol. 3217, 1425–1434. Offshore Technology Conference. <https://doi.org/10.4043/3217-MS>.
- Cartwright, P., M. K. Traver, and S. M. Sanders. 2021. "The Evolution and Development of Coloniality in Hydrozoans." *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 336: 293–299. <https://doi.org/10.1002/jez.b.22996>.
- Chávez Ortiz, E. A. 2025. *Distribución e Inventario de Algunas Especies Bentónicas (Hexacorales, Octocorales, Esponjas, y Especies Misceláneas) en Arrecifes Del Caribe Mexicano*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. <https://doi.org/10.15468/txdpn5>.
- Chávez-López, Y. 2022. "New Species of Sabellariids (Annelida: Sabellariidae) From the Caribbean Sea and the Gulf of Mexico." *European Journal of Taxonomy* 831: 109–148. <https://doi.org/10.5852/ejt.2022.831.1873>.
- Costello, M. J., P. Tsai, P. S. Wong, A. K. L. Cheung, Z. Basher, and C. Chaudhary. 2017. "Marine Biogeographic Realms and Species Endemism." *Nature Communications* 8: 1057. <https://doi.org/10.1038/s41467-017-01121-2>.
- Crisci, J. V. 2001. "The Voice of Historical Biogeography." *Journal of Biogeography* 28: 157–168. <https://doi.org/10.1046/j.1365-2699.2001.00523.x>.
- Crisci, J. V., O. E. Sala, L. Katinas, and P. Posadas. 2006. "Bridging Historical and Ecological Approaches in Biogeography." *Australian Systematic Botany* 19: 1–10. <https://doi.org/10.1071/SB05006>.
- Crother, B. I., and C. M. Murray. 2011. "Ontology of Areas of Endemism." *Journal of Biogeography* 38: 1009–1015. <https://doi.org/10.1111/j.1365-2699.2011.02483.x>.
- Cuadrado, D., A. Hernández-Gonzalez, C. Noreña, and N. Simões. 2024. "Polyclads (Platyhelminthes) in the Southern Gulf of Mexico: Unveiling Biodiversity and Descriptions of Two New Species." *ZooKeys* 1221: 103–144. <https://doi.org/10.3897/zookeys.1221.128260>.
- Culver, S. J., and M. A. Buzas. 1981. "Foraminifera Distribution of Provinces in the Gulf of Mexico." *Nature* 290: 328–329. <https://doi.org/10.1038/290328a0>.
- Daru, B. H., P. Karunarathne, and K. Schliep. 2020. "Phyloregion: R Package for Biogeographical Regionalization and Macroecology." *Methods in Ecology and Evolution* 11: 1483–1491. <https://doi.org/10.1111/2041-210X.13478>.

- Denelle, P., B. Leroy, and M. Lenormand. 2025. "Bioregionalization Analyses With the Bioregion R Package." *Methods in Ecology and Evolution* 16: 496–506. <https://doi.org/10.1111/2041-210X.14496>.
- Ebach, M. C. 2015. "The Multidisciplinary Nature of Biogeography." *Australian Systematic Botany* 28: 79–80. <https://doi.org/10.1071/SB15013>.
- Ebach, M. C., J. J. Morrone, L. R. Parenti, and Á. L. Vilorio. 2008. "International Code of Area Nomenclature." *Journal of Biogeography* 35: 1153–1157. <https://doi.org/10.1111/j.1365-2699.2008.01920.x>.
- Ebach, M. C., and L. R. Parenti. 2015. "The Dichotomy of the Modern Bioregionalization Revival." *Journal of Biogeography* 42: 1801–1808. <https://doi.org/10.1111/jbi.12558>.
- Engle, V. D., and J. K. Summers. 2000. "Biogeography of Benthic Macroinvertebrates in Estuaries Along the Gulf of Mexico and Western Atlantic Coasts 1, 2." *Hydrobiologia* 436: 17–33. <https://doi.org/10.1023/A:1026572601578>.
- Escalante, T. 2011. "De Cómo el Análisis de Parsimonia de Endemismos (PAE) Tampoco Explica la Selección Natural." *Revista Mexicana de Biodiversidad* 82: 1057–1059.
- Escalante, T. 2015. "Parsimony Analysis of Endemicity and Analysis of Endemicity: A Fair Comparison." *Systematics and Biodiversity* 13: 413–418. <https://doi.org/10.1080/14772000.2015.1046966>.
- Escobar Briones, E. G. 2025. *Crustáceos Macrobénticos de la Plataforma y Talud Continental Del Golfo de México*. Versión 1.18. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. <https://doi.org/10.15468/oxikd4>.
- Fattorini, S. 2022. "Global Patterns of Earwig Species Richness." *Diversity* 14: 890. <https://doi.org/10.3390/d14100890>.
- Ferrari, A., D. Janisch Alvares, P. M. Buratto, and K. Ribeiro Barão. 2022. "Distribution Patterns of Triatominae (Hemiptera: Reduviidae) in the Americas: An Analysis Based on Networks and Endemicity." *Cladistics* 38: 563–581. <https://doi.org/10.1111/cla.12500>.
- Fujiwara, Y., and K. Kon. 2020. "Marine Ecology: Continental Shelf to Deep Sea." In *Japanese Marine Life*, edited by K. Inaba and J. M. Hall-Spencer, 255–262. Springer.
- Glasby, C. J., C. Erséus, and P. Martin. 2021. "Annelids in Extreme Aquatic Environments: Diversity, Adaptations and Evolution." *Diversity* 13: 98. <https://doi.org/10.3390/d13020098>.
- Goloboff, P. A., and M. E. Morales. 2023. "TNT Version 1.6, With a Graphical Interface for MacOS and Linux, Including New Routines in Parallel." *Cladistics* 39: 144–153. <https://doi.org/10.1111/cla.12524>.
- Gómez-Mendicuti, R. E., C. A. Kao-Chicmul, V. M. Ojeda-Acosta, D. S. Pérez-López, L. V. León-Deniz, and J. M. Ahuatzin-Hernández. 2025. "Assessing the Distribution of Algal Biodiversity Across the Shelf Zones of the Gulf of Mexico and Adjacent Waters." *Regional Studies in Marine Science* 91: 104543. <https://doi.org/10.1016/j.rsma.2025.104543>.
- Haedrich, R. L. 1996. "Deep-Water Fishes: Evolution and Adaptation in the Earth's Largest Living Spaces." *Journal of Fish Biology* 49: 40–53. <https://doi.org/10.1111/j.1095-8649.1996.tb06066.x>.
- Hernández-Zaltrón, V., L. V. León-Deniz, and J. M. Ahuatzin-Hernández. 2025. "Biodiversity Distribution Patterns of Echinoderms From the Gulf of Mexico and Adjacent Waters: Species Richness, Beta Diversity and Endemism." *Hydrobiologia* 853: 1171–1186. <https://doi.org/10.1007/s10750-025-05987-y>.
- Hoffmeister, C. H., and A. Ferrari. 2016. "Areas of Endemism of Arthropods in the Atlantic Forest (Brazil): An Approach Based on a Metacensus Criterion Using Endemicity Analysis." *Biological Journal of the Linnean Society* 119: 126–144. <https://doi.org/10.1111/bij.12802>.
- Humphries, C. J., and L. R. Parenti. 1999. *Cladistic Biogeography (Second Edition): Interpreting Patterns of Plant and Animal Distributions*. Oxford University Press.
- Kreft, H., and W. Jetz. 2010. "A Framework for Delineating Biogeographical Regions Based on Species Distributions." *Journal of Biogeography* 37: 2029–2053. <https://doi.org/10.1111/j.1365-2699.2010.02375.x>.
- Legendre, P. 2014. "Interpreting the Replacement and Richness Difference Components of Beta Diversity." *Global Ecology and Biogeography* 23: 1324–1334. <https://doi.org/10.1111/geb.12207>.
- MacArthur, R. H., and E. O. Wilson. 1963. "An Equilibrium Theory of Insular Zoogeography." *Evolution* 17: 373–387. <https://doi.org/10.2307/2407089>.
- Monge-Nájera, J. 2008. "Ecological Biogeography: A Review With Emphasis on Conservation and the Neutral Model." *Gayana* 72: 102–112.
- Morales-Guerrero, A., T. P. Miranda, and A. C. Marques. 2017. "Comparison Between Parsimony Analysis of Endemicity (PAE), Endemicity Analysis (EA), and an Alternative Coding of Three-Distribution Statements Based on Hypothetical Distributions." *Systematics and Biodiversity* 15: 391–398. <https://doi.org/10.1080/14772000.2016.1257519>.
- Morrone, J. J. 1994. "On the Identification of Areas of Endemism." *Systematic Biology* 43: 438–441. <https://doi.org/10.2307/2413679>.
- Morrone, J. J. 2001. "Homology, Biogeography and Areas of Endemism." *Diversity and Distributions* 7: 297–300. <https://doi.org/10.1046/j.1366-9516.2001.00116.x>.
- Morrone, J. J. 2007. "Hacia Una Biogeografía Evolutiva." *Revista Chilena de Historia Natural* 80: 509–520. <https://doi.org/10.4067/S0716-078X2007000400011>.
- Morrone, J. J. 2009. *Evolutionary Biogeography: An Integrative Approach With Case Studies*. Columbia University Press.
- Morrone, J. J. 2014. "Parsimony Analysis of Endemicity (PAE) Revisited." *Journal of Biogeography* 41: 842–854. <https://doi.org/10.1111/jbi.12251>.
- Morrone, J. J. 2018. "The Spectre of Biogeographical Regionalization." *Journal of Biogeography* 45: 282–288. <https://doi.org/10.1111/jbi.13135>.
- Morrone, J. J., and J. V. Crisci. 1995. "Historical Biogeography: Introduction to Methods." *Annual Review of Ecology and Systematics* 26: 373–401.
- Muciño-Reyes, M. R., N. Simões, E. Guerra-Castro, et al. 2024. Occurrence dataset accessed via GBIF.org on 2025-08-16. *Community of Macrocrustaceans From the Mexican Sandy Beaches of the Gulf of México and Caribbean Sea Collected by the National Autonomous University of Mexico (UNAM)*. Version 1.6. Caribbean OBIS Node. <https://doi.org/10.15468/zfzt5w>.
- Neigel, J. E. 2009. "Populations Genetics and Biogeographic of the Gulf of Mexico." In *Gulf of Mexico: Origin, Waters and Biota. Biodiversity*, edited by D. L. Felder and D. K. Camp, vol. 1, 1353–1369. Texas A&M University Press.
- Nelson, G., and N. I. Platnick. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press.
- Nihei, S. S. 2006. "Misconceptions About Parsimony Analysis of Endemicity." *Journal of Biogeography* 33: 2099–2106. <https://doi.org/10.1111/j.1365-2699.2006.01619.x>.
- Oliveira, U., F. Azevedo, A. Dias, et al. 2024. "Beta Diversity and Regionalization of the Western Atlantic Marine Biota." *Journal of Biogeography* 51: 1469–1480. <https://doi.org/10.1111/jbi.14837>.
- Paradis, E., and K. Schliep. 2019. "Ape 5.0: An Environment for Modern Phylogenetics and Evolutionary Analyses in R." *Bioinformatics* 35: 526–528. <https://doi.org/10.1093/bioinformatics/bty633>.
- Paz-Ríos, C. E., D. Pech, L. F. Carrera-Parra, and N. Simões. 2021. "Biodiversity and Biogeographic Affinity of Benthic Amphipods From the Yucatan Shelf: An Analysis Across the Warm Northwest Atlantic

- Ecoregions." *Systematics and Biodiversity* 19: 928–939. <https://doi.org/10.1080/14772000.2021.1947920>.
- Pérez-Botello, A. M., and N. Simões. 2021. "Sponge-Dwelling Fauna: A Review of Known Species From the Northwest Tropical Atlantic Coral Reefs." *Biodiversity Data Journal* 9: e63372. <https://doi.org/10.3897/BDJ.9.e63372>.
- Posadas, P., J. V. Crisci, and L. Katinas. 2006. "Historical Biogeography: A Review of Its Basic Concepts and Critical Issues." *Journal of Arid Environments* 66: 389–403. <https://doi.org/10.1016/j.jaridenv.2006.01.004>.
- Ribeiro Machado, V., M. J. R. Pereira, F. P. Tirelli, V. R. Machado, D. Bennet, and A. Ferrari. 2024. "Endemism and Regionalization of Neotropical Mammals: A Multi-Taxon Analysis." *Journal of Mammalogy* 105: 792–808. <https://doi.org/10.1093/jmammal/gyae055>.
- Ricklefs, R. E., and D. G. Jenkins. 2011. "Biogeography and Ecology: Towards the Integration of Two Disciplines." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 366: 2438–2448. <https://doi.org/10.1098/rstb.2011.0066>.
- Sanmartín, I. 2012. "Historical Biogeography: Evolution in Time and Space." *Evolution: Education and Outreach* 5: 555–568. <https://doi.org/10.1007/s12052-012-0421-2>.
- Sanvicente-Añorve, L., B. V. Ramírez, and M. Hermoso-Salazar. 2023. "Pelagic Amphipods (Crustacea, Amphipoda, Hyperidea) From the Southern Gulf of Mexico With Notes on the Distribution of Species." *Biodiversity Data Journal* 11: e97347. <https://doi.org/10.3897/BDJ.11.e97347>.
- Shih, T. C., J. L. Worzel, and J. S. Watkins. 1977. "Northeastern Extension of Sigsbee Scarp, Gulf of Mexico." *American Association of Petroleum Geologist Bulletin* 61: 1962–1978. <https://doi.org/10.1306/C1EA47A2-16C9-11D7-8645000102C1865D>.
- Spalding, M. D., H. E. Fox, G. R. Allen, et al. 2007. "Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas." *Bioscience* 57: 573–583. <https://doi.org/10.1641/B570707>.
- Suzuki, R., and H. Shimodaira. 2006. "Pvclust: An R Package for Assessing the Uncertainty in Hierarchical Clustering." *Bioinformatics* 22: 1540–1542. <https://doi.org/10.1093/bioinformatics/btl117>.
- Szumik, C. A., F. Cuezco, P. A. Goloboff, and A. E. Chalup. 2002. "An Optimality Criterion to Determine Areas of Endemism." *Systematic Biology* 51: 806–816. <https://doi.org/10.1080/10635150290102483>.
- Toonen, R. J., B. W. Bowen, M. Iacchi, et al. 2016. "Biogeography, Marine." In *Encyclopedia of Evolutionary Biology*, edited by R. M. Kliman, vol. 1, 166–178. Academic Press.
- Ugalde, D., J. C. C. Fernandez, P. Gómez, et al. 2021. accessed via GBIF.org on 2025-08-16. "Porifera Diversity and Distribution Data in the Southern Gulf of Mexico." *Global Biodiversity Information Facility*. <https://doi.org/10.5281/zenodo.4563206>.
- Vilchis, M. I., K. M. Dreckmann, E. A. García-Trejo, O. E. Hernández, and A. Senties. 2018. "Patrones de Distribución de Las Grandes Macroalgas en el Golfo de México y el Caribe Mexicano: Una Contribución a la Biología de la Conservación." *Revista Mexicana de Biodiversidad* 89: 183–192. <https://doi.org/10.22201/ib.20078706e.2018.1.2226>.
- Vilhena, D. A., and A. Antonelli. 2015. "A Network Approach for Identifying and Delimiting Biogeographical Regions." *Nature Communications* 6: 6848. <https://doi.org/10.1038/ncomms7848>.
- Vital, X. G., L. A. Palomino-Alvarez, D. Ortigosa, E. J. Guerra-Castro, and N. Simões. 2023. "Sea Slugs (Gastropoda: Heterobranchia) Associated With Autonomous Reef Monitoring Structures (ARMS) in Southern Gulf of Mexico and Mexican Caribbean Sea." *Journal of the Marine Biological Association of the United Kingdom* 103: e50. <https://doi.org/10.1017/S0025315423000334>.
- Wei, C. L., G. T. Rowe, G. F. Hubbard, et al. 2010. "Bathymetric Zonation of Deep-Sea Macrofauna in Relation to Export of Surface Phytoplankton Production." *Marine Ecology Progress Series* 399: 1–14. <https://doi.org/10.3354/meps>.
- Whittaker, R. J., M. B. Araújo, P. Jepson, R. J. Ladle, J. E. M. Watson, and K. J. Willis. 2005. "Conservation Biogeography: Assessment and Prospect." *Diversity and Distributions* 11: 3–23. <https://doi.org/10.1111/j.1366-9516.2005.00143.x>.
- Wilkinson, T., E. Wiken, J. Bezaury-Creel, et al. 2009. *Ecorregiones Marinas de América Del Norte*. Comisión Para la Cooperación Ambiental.
- Williams, S. J., M. Kulp, S. Penland, et al. 2011. "Mississippi River Delta Plain, Louisiana Coast, and Inner Shelf Holocene Geologic Framework, Processes, and Resources." In *Gulf of Mexico: Origin, Waters, and Biota: Geology*, edited by N. A. Buster and C. W. Holmes, 175–193. Texas A&M University Press.
- Wolff, G., G. Rowe, M. Kennicutt, et al. 2023. "The Deepwater Program: Northern Gulf of Mexico Continental Slope Habitat and Benthic Ecology – DgoMB: Amphipods. Version 1.1." United States Geological Survey. Occurrence dataset. https://ipt-obis.gbif.us/resource?r=dgomb_amphipods&v=1.110.15468/2mjyjpj.
- Yarbu, I., and J. Contreras. 2017. "The Interplay Between Deformation, Erosion and Sedimentation in the Deep-Water Mexican Ridges Foldbelt, Western Gulf of Mexico Basin." *Basin Research* 29: 446–464. <https://doi.org/10.1111/bre.12157>.
- Zizka, A., D. Silvestro, T. Andermann, et al. 2019. "CoordinateCleaner: Standardized Cleaning of Occurrence Records From Biological Collection Databases." *Methods in Ecology and Evolution* 10: 744–751. <https://doi.org/10.1111/2041-210X.13152>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1.** Occurrence data set compiled from previous studies in the Gulf of Mexico and adjacent waters. **Data S2.** Community matrix coded with a hypothetical area implemented to conduct the parsimony analysis of endemism (PAE). **Data S3.** Congruence matrix composed of areas of endemism recovered from the PAE. **Data S4.** Areas recovered from the clustering analysis conducted on the original community matrix.