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From Shelf to Slope: Evolutionary Transition from Niche Conservatism to Lability in Western Atlantic Burrowing Shrimps

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Abstract

The latitudinal diversity gradient (LDG) is a fundamental pattern in ecology, yet its understanding in marine systems remains largely constrained by the 'tyranny' of the shallow shelf, often ignoring the bathymetric dimension of the continental margin. This study provides a three-dimensional macroecological assessment of burrowing shrimps (Axiidea and Gebiidea) along the Western Atlantic (46° N–47° S), integrating 128 species and extending the bathymetric range to 1100 m. The results reveal a robust bimodal and asymmetric LDG that transcends the coastal shelf, characterized by an extensive high-diversity plateau in the Greater Caribbean region (~10–24° N) with an absolute peak of 46 species at 17° N. The persistent 'tropical drop' (0–10° N) is linked to the eco-physiological barrier created by the massive Amazon and Orinoco River plumes. Most significantly, I document the 'Bathyal Paradox': a radical evolutionary transition where the strong niche conservatism observed in shallow waters vanishes in the deep slope, indicating that the environmental stability of the deep slope promotes niche lability and clade-specific diversification. Furthermore, a consistent inverse Rapoport pattern across the entire water column confirms that regional climatic stability, rather than latitude alone, dictates geographical range geometry. This study provides a new conceptual framework for marine biodiversity, demonstrating that the integration of deep-sea data is essential to capture the true architecture of life in the ocean.

Keywords: bathyal paradox; latitudinal diversity gradient; niche lability; continental slope; inverse Rapoport pattern

1. Introduction

The latitudinal diversity gradient (LDG), characterized by an increase in richness from the poles toward the Equator, is the most investigated and fundamental pattern in modern ecology [1–6]. For decades, the scientific community has operated under the concept of an 'idealized LDG', which assumes a single richness peak symmetrically centered at the geographic Equator [1,3,7]. However, the accumulation of high-resolution data is challenging this paradigm, revealing hemispheric asymmetries and bimodal patterns suggesting that the architecture of biodiversity is far more complex than classic models dictate [8,9]. In the marine environment, this understanding has been historically limited by what is defined here as the 'tyranny of the shallow shelf', an observational bias that ignores the bathymetric dimension of the continental margin and assumes that rules detected in shallow waters are universal for the entire ocean.

The infraorders Axiidea (ghost shrimps) and Gebiidea (mud lobsters), hereafter referred to as burrowing shrimps, comprise two monophyletic clades of decapod crustaceans

Check for updates

Academic Editor: Bert W. Hoeksema

Received: 9 July 2026
Revised: 30 July 2026
Accepted: 6 August 2026
Published: 9 August 2026

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whose primary evolutionary hallmark is a fossorial lifestyle [10–12]. These organisms represent exceptional biological models for testing macroecological rules due to their specialized habits and advanced morphological adaptations [12]. Both Axiidea and Gebiidea exhibit a body plan highly specialized for excavation, featuring anterior appendages projected forward to facilitate movement and the construction of complex gallery systems, primarily in soft sediments and even in consolidated substrates such as reefs [11]. As ecosystem engineers, these crustaceans mediate critical bioturbation processes that transform sediment geochemistry from the intertidal zone to deep-sea environments [13–16]. With a global diversity estimated at approximately 507 Axiidea and 173 Gebiidea species [17,18], these crustaceans constitute a dominant component of the benthic fauna in intertidal and subtidal systems, currently extending their presence from the coast to extreme deep-sea habitats such as hydrocarbon seeps and hydrothermal vents [11,19,20].

In the Western Atlantic, these infraorders have provided evidence for critical deviations from the idealized biodiversity model. A comprehensive study conducted on the coastal continental shelf (<200 m depth) demonstrated that the LDG for this group is markedly asymmetric and bimodal, with a primary peak in the Caribbean (10–17° N) [21], a secondary peak in northeastern Brazil (2–3° S), and a notable "tropical drop" in richness near the Equator (0–10° N). In this shallow bathymetric stratum, bottom water temperature (BWT) and salinity (BWS) were identified as dominant predictors, showing a significant phylogenetic signal (K = 0.70 and 0.52, respectively; [21]), which suggested strong niche conservatism in shallow waters. However, such conclusions might be mere artifacts of the environmental variability of coastal waters, leaving unanswered how these lineages behave in the stability of the deep ocean.

Despite these advances, a critical gap remains in our knowledge of whether the ecological and evolutionary mechanisms dictating coastal biodiversity maintain their validity as they descend the continental margin. While the shelf is a dynamic and thermally fluctuating environment, the continental slope offers a gradient of greater thermal stability but with extreme pressure conditions and scarce primary productivity that could act as a motor for evolutionary release, allowing species to break their ancestral constraints [22]. In this sense, the fundamental question is not only how many species exist, but whether the colonization of the deep sea redefines evolutionary rules and the geometry of their distributional ranges.

The present study breaks with the traditional two-dimensional vision through a three-dimensional macroecological assessment of Axiidea and Gebiidea along the Western Atlantic. By integrating an expanded dataset of 128 taxa and extending the observation range to 1100 m deep, I aim to document what is defined as the 'Bathyal Paradox': the radical evolutionary transition from shallow niche conservatism toward total niche lability in the deep slope. Through this new conceptual framework, this study seeks to demonstrate that the integration of deep-sea data is not a mere precision adjustment, but a mandatory requirement to capture the true architecture of life in the ocean.

2. Materials and Methods

2.1. Data Collection and Taxonomic Validation

To evaluate the latitudinal diversity gradient (LDG) of burrowing shrimps in the Western Atlantic, a comprehensive database was compiled documenting the northern and southern latitudinal limits and bathymetric ranges of species belonging to the infraorders Axiidea and Gebiidea. The study included all valid species recorded in the Western Atlantic, spanning a geographical extent from 46° N in Canada to 47° S in Argentine Patagonia. Information was obtained through an exhaustive review of specialized literature and fieldwork conducted along the coasts of Central and South America [23–31] and subsequently vali-

dated and strengthened by consulting records from various zoological collections, such as the National Museum of Natural History (Smithsonian Institution, USNM) and the Museu de Oceanografia Prof. Petrônio Alves Coelho at the Federal University of Pernambuco, as well as digital records integrated through the iDigBio (Integrated Digitized Biocollections) portal. This curation process allowed for the reduction in the proportion of singletons to 27% of the total sample, increasing the statistical robustness of the macroecological analyses. The taxonomic status of each taxon was verified and updated following the standards of the World Register of Marine Species (WoRMS) for the infraorders Axiidea and Gebiidea [17,18].

2.2. Latitudinal Distribution and Macroecological Metrics

Macroecological analyses initially focused on characterizing the geometry of each species' latitudinal distribution. To this end, range size was calculated as the absolute difference between the northern and southern latitudinal limits, allowing for the application of a range-through approach to estimate species richness in one-degree latitudinal bins. Simultaneously, the midpoint of each taxon, defined as the geographic center of its distribution, was identified to test the mid-domain effect (MDE) and evaluate potential deviations of the gradient toward the Caribbean or northeastern Brazil. This data structure further enabled the examination of the Range–Latitude relationship to verify Rapoport's Rule [32,33], analyzing whether latitudinal extent increases toward temperate regions in response to environmental thermal variability. Finally, a bathymetric analysis using mean depth (Z) was integrated to preliminarily evaluate how the position in the water column influences the amplitude of these latitudinal ranges. All computational procedures, data management, and visualizations were performed in the R statistical environment [v4.4.2] [34], primarily utilizing the *tidyverse* library for data manipulation and *ggplot2* for the generation of diversity gradients and scatter plots.

2.3. Analysis of the Latitudinal Diversity Gradient (LDG)

Species richness was estimated in one-degree (1°) latitudinal bins using a range-through approach, assuming the continuous presence of each taxon between its extreme northern and southern geographic limits documented in the Western Atlantic [35,36]. This approach assumes that the sampling effort is spatially homogenous, which is often not the case. Although estimates of local sampling effort are lacking across the study area, such bias should produce specific trends different from reported here. For instance, sampling effort in global databases such as the Ocean Biogeographic Information System is strongly biased towards mid-latitudes (especially in the northern hemisphere), and the tropics tend to be undersampled [37]. Because tropical areas are represented mostly by developing countries [38], sampling effort might be considerably lower in these areas [39], thus leading to spurious extra-tropical peaks of diversity [37]; this is not the case (e.g., peaks are *intra*-tropical, see Section 3). That said, I explored the potential impact of different types of sampling biases on the shape of the LDG. Analyses were carried out for higher taxonomic levels (infraorder, family), at which sampling biases are expected to be much lower than species and excluding singletons (i.e., species documented in a single locality, or with a known distribution smaller than one degree of latitude). If the LDG is independent of the level of taxonomic completeness, which may not necessarily be true [40], then the shape of the LDG should be insensitive to the discovery of new species.

This method was applied to the updated database of 128 burrowing shrimp species (infraorders Axiidea and Gebiidea), which ranges from 46° N in Canada to 47° S in Patagonia. Unlike the previous study by Hernáez et al. (2021, [21]), which was strictly limited to the coastal shelf (<200 m), the current analysis incorporated taxa inhabiting the conti-

nental slope and bathyal zones, recording mean depths of up to 1035 m (e.g., *Eiconaxius agassizi*). This expansion allowed for an evaluation of whether the previously detected gradient bimodality and tropical drop persist in strata of greater thermal stability, which are characteristic of deep-sea environments [20].

To further dissect the LDG structure, the global gradient was decomposed by infraorder, independently comparing the richness patterns of Axiidea and Gebiidea. This taxonomic breakdown enabled the identification of divergent biological responses to specific environmental filters [41], evaluating whether the 'tropical drop' (0–10° N) impacts both clades uniformly or if a differential sensitivity exists based on the unique ecophysiological adaptations of each lineage. Such sensitivity is particularly relevant concerning salinity fluctuations, which critically affect the larval dispersal of decapods [42–44] and other marine invertebrates along the Western Atlantic [45].

Additionally, I examined the interaction between latitudinal range geometry and species richness [36]. Given that an inverse Rapoport pattern has been documented for this group in the Western Atlantic, characterized by a significant increase in latitudinal extent toward lower latitudes ($r = -0.47$, $p < 0.001$; [21]), it is analyzed whether the richness peaks in the Caribbean (~10–17° N) and northeastern Brazil (~2–3° S) result from the overlap of wide-ranging tropical species or are driven by endemism centers with restricted ranges [46].

Finally, a refinement of the analysis was conducted in the equatorial region to more precisely characterize the richness drop observed between the mouths of the Amazon and Orinoco rivers [21,45]. Using updated records, I evaluated the nonlinear response of species richness to these massive freshwater discharges, ranked as the first and third most voluminous on the planet, respectively [47], which act as osmotic barriers that condition larval survival [42–44] and limit the dispersal of marine populations in the Western Atlantic [45,48].

2.4. Environmental Modeling and Determinants of Diversity and Bathymetric Distribution

To evaluate the relative importance of environmental factors in shaping the Latitudinal Diversity Gradient (LDG) and vertical community structure, a Random Forest (RF) regression analysis was implemented [49]. This machine learning method was selected due to its high predictive accuracy, exceeding 92% of explained variance in previous assessments of this group [21], as well as its capacity to model complex non-linear relationships and its inherent robustness against overfitting when dealing with large-scale biogeographic datasets [50,51].

Unlike previous analyses limited to the continental shelf [21], this model utilized an expanded database of 128 species distributed from the intertidal zone to the continental slope (1100 m depth). Based on evidence that only a subset of variables significantly drives the richness of these crustaceans, four key environmental predictors were selected from standardized bioclimatic layers [52]: mean bottom water temperature (BWT, defined as the mean thermal condition at the water–sediment interface), bottom water salinity (BWS, defined as the mean salinity condition at the water–sediment interface), seasonal thermal range (BWTR, defined as the difference between the maximum and minimum annual temperature recorded at the water–sediment interface), and mean primary productivity (Primary_Prod, defined as the average rate of organic carbon production in the water column). The remaining six variables employed in the study by Hernáez et al. (2021; [21]) (e.g., pH, shelf area, coastline length) were discarded due to their low marginal contribution to the model and to prioritize variables with a clear ecophysiological signal in the deep-sea gradient [21,53].

To capture the vertical dimension of biodiversity, mean depth (Z_{mean}) was incorporated, calculated independently for the infraorders Axiidea and Gebiidea within each

latitudinal band. Environmental data were averaged over one-degree latitudinal bins using a bathymetric mask ranging from 0 to 1100 m [52] to accurately reflect the thermal and chemical conditions, such as the 4.89 °C detected at the deep Equator, encountered by slope species. This approach effectively avoids the bias of using exclusive shallow-shelf averages, which has been identified as a critical limitation in previous macroecological studies [21].

The random forest was constructed with 10,000 trees to ensure convergence and stability of the importance estimates [49]. Optimal hyperparameters were applied, including mtry = p/3 (where p represents the number of predictors) and a minimum node size of 5 [50]. Collinearity among variables was rigorously controlled through a variance inflation factor (VIF) test, maintaining only those predictors with VIF < 10 [21,54].

Three model configurations were executed to address system complexity. First, a total richness model was developed to evaluate the general drivers of the LDG across the Western Atlantic continental margin [21]. Second, a clade-specific model (Axiidea vs. Gebiidea) was implemented to identify divergences in their ecological niches, considering the deep morphological and evolutionary differences separating both groups [10,12,55]. Finally, a vertical distribution model was constructed using mean depth (Z_{mean}) as the response variable to identify the environmental determinants driving community structuring toward the continental slope and the deep ocean [22].

Variable importance was quantified via the percentage increase in Mean Squared Error (%IncMSE), a robust parameter for identifying predictors with the greatest weight in the LDG architecture [49,50]. Finally, partial dependence plots were employed to identify critical tolerance thresholds [56], enabling a discussion on how bottom water temperature (BWT) and salinity (BWS) act as metabolic barriers along the deep-sea gradient of the Western Atlantic [22,42,43].

3. Results

3.1. Geometric Properties of Latitudinal Ranges and Bathymetric Analysis

The analysis of the relationship between latitudinal range size and the absolute latitude of the midpoint revealed a significant departure from Rapoport's Rule for Western Atlantic burrowing shrimps. This trend, characterized by a contraction of geographical ranges toward higher latitudes, is defined here as an inverse Rapoport pattern. A moderate but highly significant negative correlation ($r = -0.48$, $p < 0.001$) was detected for the total sample of 128 species (Figure 1). This pattern indicates that species with distribution centers in tropical and subtropical bands possess wider geographical ranges than taxa restricted to high latitudes. Sensitivity analysis excluding taxa with exceptional ranges, such as *Cheramus profundus* (50.8°), confirmed the robustness of this trend ($r = -0.46$, $p < 0.001$). When segmented by bathymetric zone, both shelf ($r = -0.47$, $p < 0.001$) and deep slope ($r = -0.49$, $p < 0.001$) species maintained this inverse relationship, demonstrating that the increase in bottom water temperature range (BWTR) toward the poles acts as a restrictive filter across the entire water column (Figure 1). Finally, visual analysis via singleton faceting confirmed that the negative slope of the regression is driven by species with established ranges (non-singletons), providing a robust biological signal that remains statistically significant ($p < 0.001$) despite the inherent variance of macroecological datasets, whereas unique records (27% of the total sample) cluster consistently at the base of the latitudinal range axis (Figure 1).

The analysis of the latitudinal diversity gradient (LDG) for Western Atlantic burrowing shrimps ($n = 128$) revealed a statistically significant ($p < 0.001$) structure marked by hemispheric asymmetry and intra-tropical modality (Figure 2). Species richness increased significantly toward low latitudes, reaching an extensive high-diversity plateau in the greater Caribbean region (~10–24° N). Within this range, an absolute maximum peak of

46 species was recorded at 17° N, maintaining exceptional richness values (≥36 species) across 14 degrees of latitude. This massive accumulation of taxa in the Northern Hemisphere contrasts sharply with the temperate southern margin, where richness is an order of magnitude lower (e.g., 3 species at 30° S). A secondary diversity peak was consistently located in Northeastern Brazil (~2–3° S), and its mean location was statistically different from the null expectation of the Equatorial line (0°), proving that the highest accumulation of species is not centered on the geographic Equator (Figure 2). This bimodal structure is further visualized through a geographical projection to better characterize the spatial extent of the richness peaks (Figure 2).

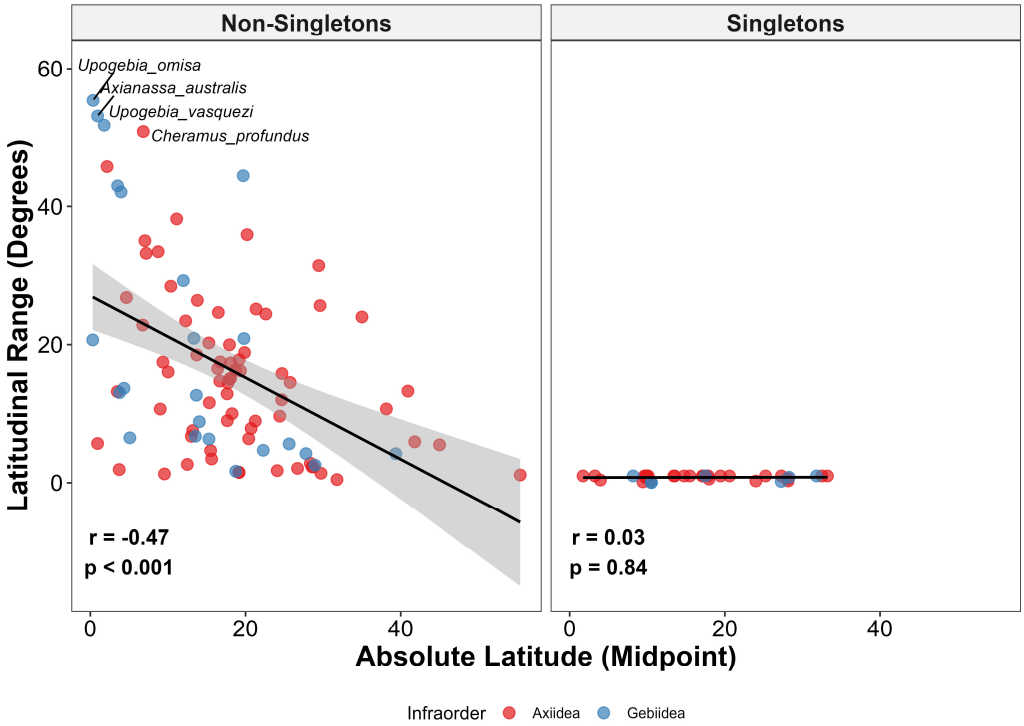

Figure 1. Relationship between latitudinal range size and absolute latitude of the midpoint for 128 burrowing shrimp species (Axiidea and Gebiidea) along the Western Atlantic coast (0–1100 m). The left panel shows a significant negative correlation for non-singleton species ($r = -0.47$, $p < 0.001$), indicating a departure from Rapoport's rule as latitudinal extent increases significantly towards the tropics. The right panel displays singletons (representing 27% of the total sample) clustered at the base of the latitudinal extent axis. Points are color-coded by infraorder: Axiidea (red) and Gebiidea (blue). The shaded area represents the 95% confidence Interval.

Between both peaks, a marked and statistically significant ($p < 0.001$) "tropical drop" in richness was observed between 0° and 10° N, coinciding with the zone of influence of the massive freshwater discharges from the Amazon and Orinoco rivers (Figure 2). The breakdown by infraorder showed that both Axiidea and Gebiidea contribute to this bimodal structure, although Axiidea exhibited higher absolute richness across all latitudinal bands (Figure 3). Notably, the inclusion of upper slope and bathyal species (>200 m depth) did not smooth out the diversity crests; on the contrary, it confirmed that bimodality is a robust property of this fauna that persists down to 1100 m depth. This spatial discontinuity is further visualized through the geographical projection in Figure 2, which links the richness decline directly to the position of the major river plumes along the Western Atlantic margin.

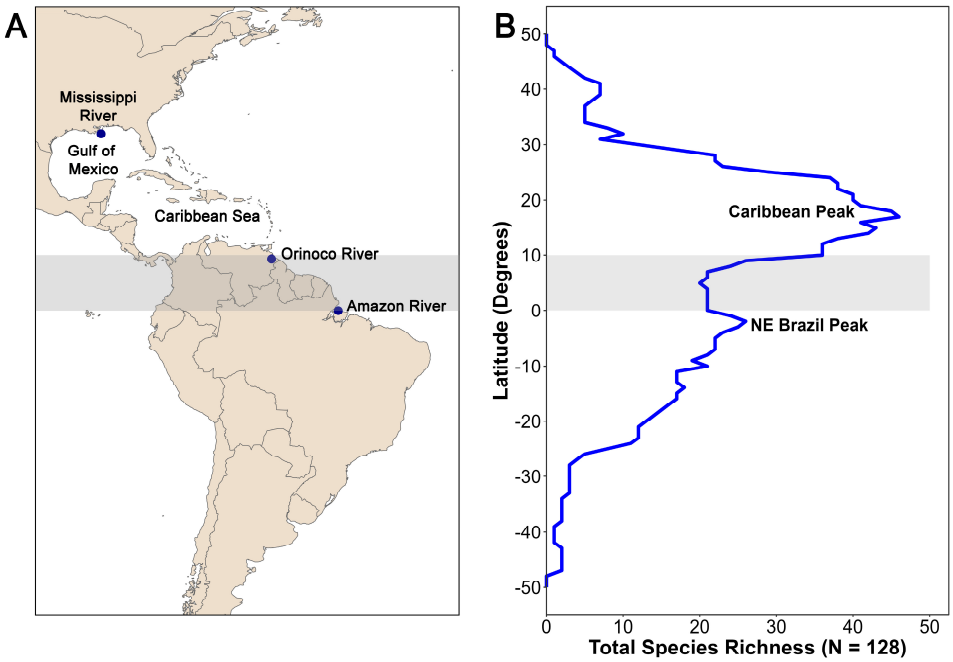

Figure 2. Integrated latitudinal diversity gradient for Western Atlantic burrowing shrimps (n = 128), encompassing a bathymetric range from the intertidal zone to the continental slope (0–1100 m depth). (**A**) Geographical projection highlighting major continental-scale river plumes (Mississippi, Orinoco, and Amazon) and the habitat complexity of the Caribbean Sea. (**B**) Total species richness showing a robust bimodal structure: an extensive high-diversity plateau in the Greater Caribbean region (~10–24° N), with an absolute maximum peak of 46 species at 17° N, and a secondary peak in Northeastern Brazil (~2–3° S). The shaded area (0–10° N) indicates the 'tropical drop' in richness, aligned with the eco-physiological barrier created by the South American river plumes.

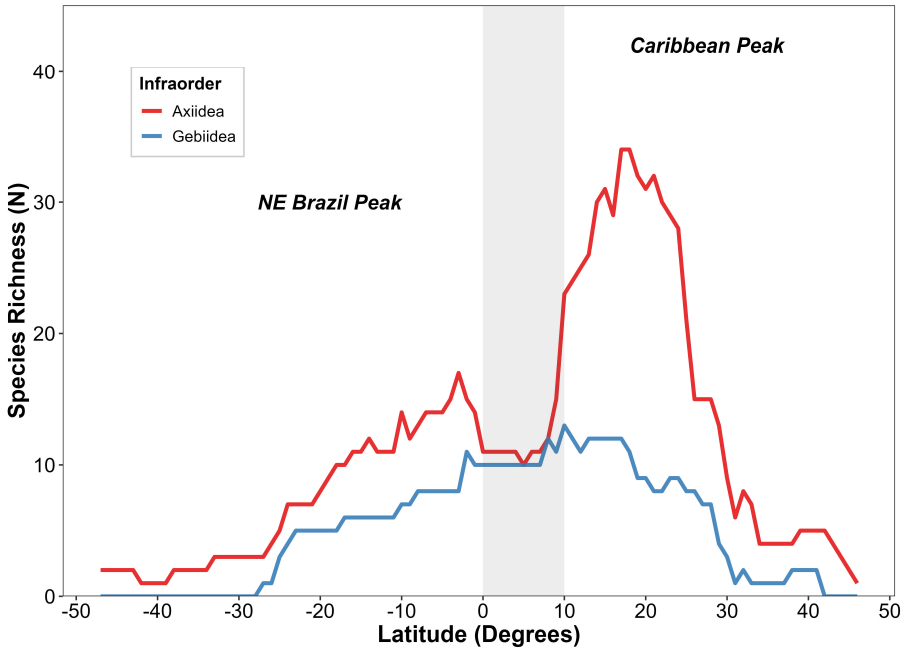

Figure 3. Latitudinal Diversity Gradient (LDG) of burrowing shrimps (Axiidea and Gebiidea) along the Western Atlantic continental margin. Species richness (N) is estimated in 1° latitudinal bins using a range-through approach, integrating taxa from the shelf to the continental slope (up to 1100 m depth). The gradient reveals a statistically significant ($p < 0.001$) bimodal intra-tropical structure, featuring a primary peak in the Caribbean Sea (~10–17° N) and a secondary peak in Northeastern Brazil

(~2–3° S). The shaded area (0–10° N) indicates the 'tropical drop' in richness, coinciding with the massive freshwater discharges of the Amazon and Orinoco Rivers. This bimodal structure is integrated with a geographical projection to visualize the spatial extent of the richness peaks and the tropical discontinuity along the coastline. Lines represent the independent contribution of each infraorder.

3.2. Environmental Modeling and Determinants of Biodiversity

The Random Forest (RF) model applied to the total richness of the 128 analyzed taxa showed high predictive accuracy, explaining 86.61% of the variance (Figure 4). The variable importance ranking, quantified via the percentage increase in mean squared error (%IncMSE), identified bottom water temperature (BWT) as the dominant predictor (127.40), followed by seasonal thermal range (BWTR: 114.65) and bottom water salinity (BWS: 108.97) (Table 1A; Figure 4A). Primary productivity (Primary_Prod) provided the lowest relative contribution, with a %IncMSE of 88.05. These results are supported by a thermal gradient that, by integrating the continental slope, registers BWT values as low as 4.89 °C at equatorial latitudes (0°), reflecting the transition to deep-water conditions across the expanded bathymetric range (0–1100 m depth) (Figure 4B,C).

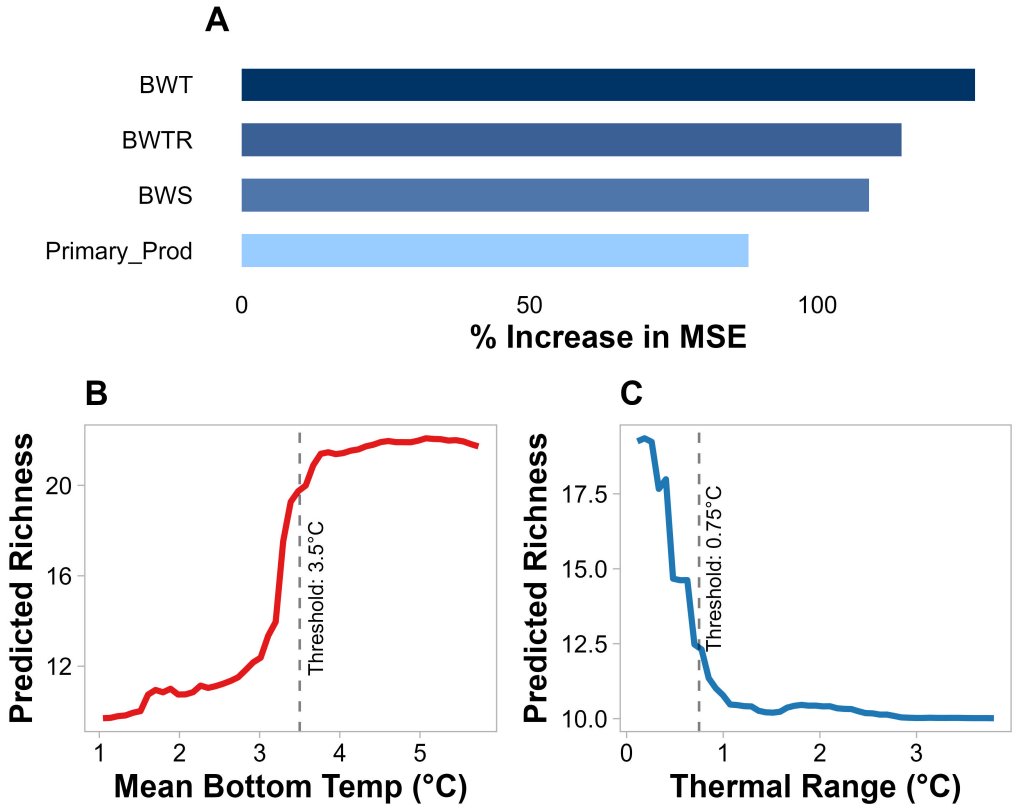

Figure 4. Random Forest (RF) model results for burrowing shrimp species richness along the Western Atlantic continental margin (0–1100 m; N = 128). (**A**) Variable importance ranking expressed as the percentage increase in Mean Squared Error (%IncMSE). Mean bottom water temperature (BWT: 127.40) and seasonal thermal range (BWTR: 114.65) are the dominant predictors of biodiversity architecture. (**B**) Partial dependence plot for BWT. A vertical jump in predicted richness occurs at the 3.5 °C critical threshold, providing visual evidence of the "Bathyal Paradox": the evolutionary transition from niche conservatism toward niche lability in the deep slope. (**C**) Partial dependence plot for BWTR. Richness collapses abruptly when thermal instability exceeds 0.75 °C, confirming an "Anti-Rapoport" pattern where regional climatic stability dictates geographical range geometry. Rugs along the X-axis represent observed data distribution. The model explains 86.61% of total variance (10,000 trees, *nodesize* = 5).

Table 1. Environmental predictors of the latitudinal diversity gradient of burrowing shrimps along the Western Atlantic coast, integrating for the first time data from both the continental shelf and slope (0–1100 m). These predictors serve as proxies for various hypotheses grouped into three conceptual categories: ecological limits, diversification dynamics, and time for species accumulation (sensu [57]). The table details the level of collinearity via the Variance Inflation Factor (VIF) and the relative importance of variables through the percentage increase in Mean Squared Error (%IncMSE) derived from the Random Forest analysis. Results are presented for the total richness model (**A**) and specific clade models ((**B**): Axiidea; (**C**): Gebiidea), the latter of which includes both species richness and mean depth (Z_{mean}) to reflect dimensions beyond simple richness. Additionally, the phylogenetic signal (Blomberg's *K*) is reported to assess the transition from niche conservatism in shallow waters to niche lability in deep-sea habitats. Significant values ($p < 0.05$) are highlighted in bold. [a] Temperature-dependent speciation. [b] Niche conservatism. [c] Seasonal coexistence. [d] Climatic stability (decades to millennia). [e] Climatic stability (millennia to millions of years). [f] More individuals: carrying capacity. [g] More specialization.

A Predictor	Ecological Limits	Diversification Dynamics	Time for spp Accumulation	VIF	Relative Importance (%IncMSE)		Phylogenetic Signal (K)	*p*-Value (K)
					Richness	Depth (Z_{mean})		
Mean bottom water temperature (BWT)	c, d	a	b	3.24	127.40	--	0.035	0.062
Bottom water temperature range (BWTR)		e	b	3.41	114.65	--	0.022	0.934
Mean bottom water salinity (BWS)			b	4.92	108.97	--	0.037	**0.013**
Mean primary productivity	f, g		b	1.45	88.05	--	0.029	0.270
Explained variance: 86.61%								
B								
Mean bottom water temperature (BWT)	c, d	a	b	3.07	113.39	75.26	0.040	0.255
Bottom water temperature range (BWTR)		e	b	3.40	98.83	67.48	0.039	0.339
Mean bottom water salinity (BWS)			b	4.81	104.78	77.44	0.038	0.425
Mean primary productivity	f, g		b	1.49	81.16	51.99	0.033	0.872
Explained variance: Richness (84.15%) | Depth (62.57%)								
C								
Mean bottom water temperature (BWT)	c, d	a	b	2.42	143.52	133.09	0.174	0.215
Bottom water temperature range (BWTR)		e	b	1.42	129.59	78.07	0.161	0.322
Mean bottom water salinity (BWS)			b	3.98	113.35	102.03	0.161	0.297
Mean primary productivity	f, g		b	2.63	100.22	85.28	0.118	0.717
Explained variance: Richness (87.28%) | Depth (79.58%)								

When disaggregating richness by clade, salinity (BWS: 104.78) displaced BWTR (98.83) as the second most influential predictor for Axiidea (explained variance: 84.15%) after BWT (113.39) (Table 1B). In contrast, the model for Gebiidea reached an explained variance of 87.28%, maintaining a predictor hierarchy consistent with the total model: BWT (143.52) >> BWTR (129.59) >> BWS (113.35) >> Primary_Prod (100.22) (Table 1C). Regarding the modeling of mean depth (Z_{mean}), a divergence in slope occupation was observed: for Gebiidea, the model explained 79.58% of the variance with BWT as the dominant factor (133.09% IncMSE), whereas for Axiidea, the explained variance was 62.57%, with salinity (BWS: 77.44) slightly outperforming BWT (75.26) (Table 1B,C).

Phylogenetic signal analysis for the 128 species across the expanded gradient (0–1100 m depth) revealed consistently low Blomberg's *K* values for the main predictors. For bottom water temperature, the signal was not statistically significant (BWT:

$K = 0.035$, $p = 0.062$), indicating an evolutionary transition toward niche lability within the studied bathymetric gradient. Conversely, salinity maintained a statistically significant but extremely weak phylogenetic signal (BWS: $K = 0.037$, $p = 0.013$) (Table 1A).

Finally, disaggregating the analysis by clade consistently confirmed the loss of the phylogenetic signal detected in the global model. For Axiidea (Table 1B), Blomberg's K values for temperature and salinity were extremely low and non-significant (BWT: $K = 0.040$, $p = 0.255$; BWS: $K = 0.038$, $p = 0.425$), reinforcing the hypothesis of a flexible adaptation to slope conditions. An identical pattern was observed in Gebiidea (Table 1C), where despite showing slightly higher K values, none reached statistical significance (BWT: $K = 0.174$, $p = 0.215$; BWS: $K = 0.161$, $p = 0.297$). This demonstrates that both lineages have been released from their evolutionary constraints upon colonizing the deep bathymetric gradient. Taken together, these findings demonstrate that niche lability is a widespread phenomenon among Western Atlantic burrowing shrimps as they expand their geographical and bathymetric ranges along the continental margin.

4. Discussion

4.1. Geometric Properties of Latitudinal Range and Bathymetric Analysis

The analysis of latitudinal range geometry for Western Atlantic burrowing shrimps revealed a definitive departure from Rapoport's Rule [32,33]. A moderate but highly significant negative correlation ($r = -0.48$, $p < 0.001$) was detected for the total sample of 128 species, indicating an inverse Rapoport pattern where tropical and subtropical species possess wider geographic ranges than high-latitude taxa. This finding is consistent with that previously reported by Hernáez et al. (2021; [21]) for coastal shelf Axiidea and Gebiidea in the Western Atlantic ($r = -0.47$) and those reported in other groups [58] but demonstrates that the trend not only persists but remains robust when integrating continental slope and bathyal species ($r = -0.49$, $p = 0.017$). The primary driver of this range restriction toward temperate regions (46° N and 47° S) is the increase in seasonal thermal range (BWTR), which acts as an implacable ecophysiological filter limiting poleward species expansion [21,33]. Conversely, the thermal stability characteristic of tropical bands and the deep slope [22] allows for exceptional cases such as *Cheramus profundus*, which attains a massive latitudinal extent of ~50.8° despite inhabiting a mean depth of 423.5 m. This suggests that regional climatic stability is the ultimate factor dictating the geographic range size of these crustaceans across the entire water column.

A critical aspect ensuring the integrity of these results is the evaluation of the impact of singletons on range geometry. Although these unique records—species documented in a single locality or with ranges smaller than 1°—represent 27% of the total sample (35 of 128 species), their distribution lacks a significant latitudinal signal ($r = 0.03$, $p = 0.84$), clustering predictably at the base of the latitudinal extent axis. However, the exclusion of these taxa in sensitivity analyses did not weaken the general pattern; on the contrary, it confirmed that the inverse Rapoport trend (i.e., the reduction in geographical range size toward high latitudes) is a robust biological property driven by species with established ranges (non-singletons), which maintain a negative correlation of $r = -0.46$ ($p < 0.001$) even after singleton removal. This statistical safeguard allows us to rule out the possibility that the observed gradient is an artifact derived from sampling biases or the inclusion of rare species [21,37], reinforcing the conclusion that climatic stability at low latitudes and deep slope is the actual mechanism enabling geographical range expansion in the Western Atlantic.

4.2. The Latitudinal Diversity Gradient (LDG): Bimodality and the Tropical Drop

The Latitudinal Diversity Gradient (LDG) obtained for the 128 analyzed taxa confirms a bimodal and asymmetrical structure, substantially validating and strengthening the pattern previously detected for the coastal shelf [21]. A fundamental finding of this bathymetric expansion is that the primary peak in the Northern Hemisphere does not constitute an isolated point, but rather an extensive high-diversity plateau located in the greater Caribbean region (~10–24° N). Within this range, species richness reached an absolute apex of 46 species at 17° N, maintaining exceptional values (≥36 species) across 14 degrees of latitude. The geographical location of this maximum richness value contrasted with that reported by Hernáez et al. (2021; [21]), who recorded a maximum richness of 35 species at 10° N. The massive accumulation of taxa reported here represents a nearly fourfold increase compared to northern extratropical zones, and it is an order of magnitude higher than the richness documented along the temperate southern margin (e.g., 3 species at 30° S). The persistence of this structure when including continental slope species (down to 1100 m) demonstrates that bimodality is a robust biological property that transcends the shelf and is maintained in strata of greater thermal stability, such as those of the tropical region. This bimodal latitudinal diversity gradient (LDG) has also been observed in other marine crustaceans, including burrowing shrimps from other regions of the world, with the difference that in those studies, one of the two modes was recorded outside the tropical region [59–61]. While the phenomenon of extratropical LDG bimodality could be attributed to sampling insufficiency in the tropics [37,62,63], the present analyses suggest that intra-tropical bimodality is not attributable to sampling biases or taxonomic completeness, representing a true biological pattern for Western Atlantic burrowing shrimps, as previously reported by Hernáez et al. (2021; [21]).

Between the Caribbean plateau and the secondary peak in Northeastern Brazil (~2–3° S), the persistence of the 'tropical drop' (0–10° N) constitutes the most significant deviation from the idealized equatorial model detected in this study. This dramatic decline in richness is directly linked to the massive freshwater discharges of the Amazon and Orinoco rivers, ranked globally as the first and third in terms of water volume released into the ocean [47]. These river plumes act as critical osmotic and ecophysiological barriers that condition the survival of decapod larval phases [42]. The literature suggests that the extreme reduction in salinity within these areas of fluvial influence triggers larval mortality and limits effective population dispersal [42–44], creating a biogeographical discontinuity that affects both coastal fauna and deep continental margin assemblages [45,48]. The results demonstrate that both Axiidea and Gebiidea are sensitive to this freshwater 'wall', confirming that the configuration of the LDG in the Western Atlantic is dictated by oceanographic processes at a continental scale that override the simple effect of latitude, even in slope strata where thermal stability is higher.

Complementing the massive influence of South American rivers, the northern boundary of the Caribbean region is conditioned by the Mississippi River plume and the oceanographic complexity of the Strait of Florida [47]. While the Amazon and Orinoco rivers create an equatorial osmotic 'wall' [21,42–45,47,48], the Mississippi discharge, interacting with the intense hydrodynamics of the Florida Current and steep bathymetric gradients, acts as a northern selective filter for deep-sea biota [47]. This northern barrier effect is supported by historical benthic surveys conducted by Texas A&M University (1965–1990) and records from the USNM (accessible via iDigBio), which indicate that these conditions limit the connectivity between the Gulf of Mexico and the wider West Atlantic slope. By integrating the Mississippi alongside the Amazon and Orinoco plumes, this study provides a comprehensive three-dimensional architecture of the Western Atlantic LDG, where

continental-scale fluvial discharges and current systems dictate species dispersal across both shelf and bathyal strata.

4.3. Niche Dynamics: The Bathyal Paradox and Clade-Specific Drivers

The central and most disruptive discovery of this study is the phenomenon it is defined as the 'Bathyal Paradox'. The results revealed a drastic contrast between the evolutionary mechanisms operating on the coast versus those on the continental slope. While a strong niche conservatism dictated by evolutionary heritage exists on the coastal shelf (<200 m), with robust phylogenetic signals for both temperature (K = 0.70 for BWT; [21]) and salinity (K = 0.52; [21]), the colonization of the deep slope marks the near-total fading of this phylogenetic signal (K = 0.035, p = 0.062; present study). This evidence suggests that the thermal stability and environmental homogeneity of the deep ocean [22] act as a mechanism that 'releases' lineages from their ancestral restrictions. It is proposed that, unlike coastal waters where variability forces the maintenance of inherited traits, the calm of the deep sea allows for niche lability and a flexible adaptation at great depths [64], enabling lineages to diversify ecophysiologically beyond their ancestral constraints.

However, this evolutionary release does not follow a uniform path, revealing divergent 'environmental compasses' depending on the analyzed clade. The Random Forest models for mean depth (Z_{mean}) demonstrate that the vertical structuring of the community is governed by distinct filters for each lineage. In Gebiidea, an absolute and dominant dependence on bottom water temperature (BWT) was detected, which explained their distribution on the slope with a massive importance of 133.09% IncMSE. Conversely, Axiidea displayed a unique sensitivity to bottom water salinity (BWS), a factor that displaces temperature as the strongest predictor (77.44% IncMSE) in determining their position within the deep-water column. This divergence suggests that, although both groups have achieved niche lability in the deep sea, their evolutionary histories, possibly linked to estuarine origins for Axiidea, still condition how they interact with the physicochemical properties of water when colonizing the deep continental margin. These findings confirm that the transition toward the deep slope does not completely erase the evolutionary footprints of these crustaceans but rather reconfigures them under the scenario of thermal stability of the deep ocean [22,55].

5. Conclusions

The present study represents the most ambitious macroecological assessment conducted to date for Western Atlantic burrowing shrimps, integrating for the first time the bathymetric dimension of the continental slope down to a depth of 1100 m depth. The results confirm that the bimodal Latitudinal Diversity Gradient (LDG) is not an artifact of the shallow shelf, but rather a robust biological property that manifests as an extensive high-diversity plateau in the Greater Caribbean (~10–24° N) with an absolute peak of 46 species at 17° N, whose biogeographical boundary is dictated by the ecophysiological 'wall' of the Amazon and Orinoco river plumes.

The most disruptive finding of this research is the 'Bathyal Paradox', which documents the radical transition from a strong niche conservatism in coastal waters (K = 0.70) toward total niche lability on the deep slope ($K \approx 0.03$), suggesting that the environmental stability of the deep sea acts as an engine for evolutionary release, enabling the clades Axiidea and Gebiidea to diversify beyond their ancestral constraints. Finally, the persistence of an inverse Rapoport pattern across the entire water column confirms that regional climatic stability is the determining factor governing geographical range sizes. This forces the scientific community to overcome the 'tyranny of the shallow shelf' and integrate deep-sea data to capture the true architecture of ocean life within a three-dimensional macroecology.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: The author wishes to express his gratitude to Marcelo A. A. Pinheiro for his continuous support during the postdoctoral program, which enabled the compilation of a vast amount of biogeographical data along the Brazilian coast. Special thanks are due to Marcos Tavares, curator of the crustacean collection at the Museu de Zoologia, Universidade de São Paulo (MZUSP), and to Jesser F. Souza-Filho, curator of the Museu de Oceanografia Prof. Petrônio Alves Coelho, Universidade Federal de Pernambuco (MOUFPE), for providing access and facilitating the examination of the burrowing shrimp material from Brazil. Additionally, the author sincerely thanks all the technicians from both zoological collections for their valuable assistance and support.

Conflicts of Interest: The author declares no conflicts of interest.

References

1. Pianka, E.R. Latitudinal gradients in species diversity: A review of concepts. *Am. Nat.* **1966**, *100*, 33–46. [CrossRef] [PubMed]
2. Willig, M.R.; Kaufman, D.M.; Stevens, R.D. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **2003**, *34*, 273–309. [CrossRef]
3. Hillebrand, H. On the generality of the latitudinal diversity gradient. *Am. Nat.* **2004**, *163*, 192–211. [CrossRef] [PubMed]
4. Hillebrand, H. Strength, slope and variability of marine latitudinal gradients. *Mar. Ecol. Prog. Ser.* **2004**, *273*, 251–267. [CrossRef]
5. Kinlock, N.L.; Prowant, L.; Herstoff, E.M.; Foley, C.M.; Akin-Fajiye, M.; Bender, N.; Umarani, M.; Ryu, H.Y.; Şen, B.; Gurevitch, J. Explaining global variation in the latitudinal diversity gradient: Metaanalysis confirms known patterns and uncovers new ones. *Glob. Ecol. Biogeogr.* **2018**, *27*, 125–141. [CrossRef]
6. Menegotto, A.; Kurtz, M.N.; Lana, P.D.C. Benthic habitats do show a significant latitudinal diversity gradient: A comment on Kinlock et al. (2018). *Glob. Ecol. Biogeogr.* **2019**, *28*, 1712–1717. [CrossRef]
7. Pianka, E.R. Latitudinal gradients in species diversity. *Trends Ecol. Evol.* **1989**, *4*, 223. [CrossRef]
8. Brayard, A.; Escarguel, G.; Bucher, H. Latitudinal gradient of taxonomic richness: Combined outcome of temperature and geographic mid-domains effects? *J. Zool. Syst. Evol. Res.* **2005**, *43*, 178–188. [CrossRef]
9. Rivadeneira, M.M.; Poore, G.C.B. Latitudinal gradient of diversity of marine crustaceans: Towards a synthesis. In *The Natural History of the Crustacea*; Poore, G.C.B., Thiel, M., Eds.; Oxford University Press: Oxford, UK, 2020; Volume 8, pp. 405–428.
10. de Saint Laurent, M. Vers une nouvelle classification des Crustaces Decapodes Reptantia. *Bull. Off. Natl. Pêch. Tunis.* **1979**, *3*, 15–31. [CrossRef]
11. Dworschak, P.C.; Felder, D.L.; Tudge, C.C. Infraorders Axiidea de Saint Laurent, 1979 and Gebiidea de Saint Laurent, 1979 (formerly known collectively as Thalassinidea). In *Treatise on Zoology—Anatomy, Taxonomy, Biology. The Crustacea*; Schram, F.R., von Vaupel Klein, J.C., Forest, J., Charmantier-Daures, M., Eds.; Brill: Leiden, The Netherlands, 2012; Volume 9, Part B, pp. 109–219.
12. Hernáez, P. An update on reproduction in ghost shrimps (Decapoda: Axiidea) and mud lobsters (Decapoda: Gebiidea). In *Marine Ecology*; Türkoğlu, M., Önal, U., Ismen, A., Eds.; IntechOpen: London, UK, 2018; Chapter 11, pp. 231–253.
13. Griffis, R.B.; Suchanek, T.H. A model of burrow architecture and trophic modes in thalassinidean shrimp (Decapoda: Thalassinidea). *Mar. Ecol. Prog. Ser.* **1991**, *79*, 171–183. [CrossRef]
14. Berkenbusch, K.; Rowden, A.A. Ecosystem engineering-moving away from 'just-so' stories. *Mar. Ecol.* **2003**, *27*, 67–73.
15. Bertics, V.J.; Sohm, J.A.; Treude, T.; Chow, C.-E.T.; Capone, D.G.; Fuhrman, J.A.; Ziebis, W. Burrowing deeper into benthic nitrogen cycling: The impact of bioturbation on nitrogen fixation coupled to sulfate reduction. *Mar. Ecol. Prog. Ser.* **2010**, *409*, 1–15. [CrossRef]
16. Ziebis, W.; Forster, S.; Huettel, M.; Jørgensen, B. Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. *Nature* **1996**, *382*, 619–622. [CrossRef]
17. WoRMS Editorial Board. Axiidea. World Register of Marine Species. 2026. Available online: https://www.marinespecies.org/aphia.php?p=taxdetails&id=477324 (accessed on 2 July 2026).
18. DecaNet Eds. Gebiidea. World Register of Marine Species. 2026. Available online: https://www.marinespecies.org/aphia.php?p=taxdetails&id=477323 (accessed on 2 July 2026).
19. Kensley, B. A new species of the axiid shrimp genus *Acanthaxius* from the Caribbean (Crustacea: Decapoda: Thalassinidea). *Proc. Biol. Soc. Wash.* **1996**, *109*, 70–74.

20. Felder, D.L.; Kensley, B. A new species of axiid shrimp from chemosynthetic communities of the Louisiana continental slope, Gulf of Mexico (Crustacea: Decapoda: Thalassinidea). *Proc. Biol. Soc. Wash.* **2002**, *117*, 68–75.
21. Hernáez, P.; Fenberg, P.B.; Rivadeneira, M.M. Departing from an ideal: An asymmetric, bimodal and non-Equatorial latitudinal gradient of marine diversity in Western Atlantic burrowing shrimps (Decapoda: Axiidea and Gebiidea). *J. Biogeogr.* **2021**, *48*, 650–661. [CrossRef]
22. Gage, J.D.; Tyler, P.A. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*; Cambridge University Press: Cambridge, UK, 1991.
23. Hernáez, P.; Hereman, M.J.; Pimenta, C.E.R.; Rio, J.P.P.; João, M.C.A.; Pinheiro, M.A.A. La efectividad de una ley de protección al servicio de la conservación de un recurso marino: El ejemplo del camarón fantasma *Callichirus major* (Decapoda, Callianassidae) de la costa de Brasil. *Iheringia Ser. Zool.* **2019**, *109*, e2019001. [CrossRef]
24. Hernáez, P.; Windsor, A.M.; Paula, C.A.; Santana, W. A new species of the ghost shrimp genus *Neocallichirus* Sakai, 1988 (Decapoda: Axiidea: Callianassidae) from the southwestern Atlantic. *Mar. Biol. Res.* **2020**, *16*, 50–60. [CrossRef]
25. Hernáez, P.; Miranda, M.S.; Tavares, M. A new species of *Biffarius* Manning & Felder, 1991 (Decapoda: Axiidea: Callianassidae) from the intertidal coast of northeastern Brazil. *Zootaxa* **2020**, *4759*, 575–583. [CrossRef] [PubMed]
26. Hernáez, P.; Miranda, M.S.; Rio, J.P.P.; Pinheiro, M.A.A. A new *Callichirus* ghost shrimp species from the south-western Atlantic, long confounded with *C. major* (Say, 1818) (Decapoda: Axiidea: Callichiridae). *J. Nat. Hist.* **2022**, *56*, 533–563. [CrossRef]
27. Hernáez, P.; Mugnai, R.; Souza-Filho, J.F.; Pinheiro, M.A.A. Monogamy in the burrowing shrimp *Axianassa australis* Rodrigues & Shimizu, 1992 (Decapoda, Gebiidea, Axianassidae). *Biol. Bull.* **2022**, *242*, 87–96. [CrossRef] [PubMed]
28. Hernáez, P.; Pinheiro, M.A.A.; Alves-Junior, F.A.; Santana, W. Intertidal burrowing shrimps (Axiidea: Callianassidae, Callichiridae; Gebiidea: Axiannassidae, Upogebiidae) collected along the Brazilian coast. *Mar. Biol. Res.* **2022**, *18*, 380–408. [CrossRef]
29. Hernáez, P.; Forbes, A.; de Souza, P.R.C.M.; Souza-Filho, J.F. Unraveling the mating system of the burrowing shrimp *Lepidophthalmus siriboia* (Decapoda Callichiridae) based on life history traits. *Ethol. Ecol. Evol.* **2024**, *36*, 150–174. [CrossRef]
30. Hernáez, P.; Souza-Filho, J.F. The Axiidea in the museum of oceanography Petrônio Alves Coelho, Recife, Brazil, with some remarks on the biology of the species. *Taxonomy* **2024**, *4*, 354–367. [CrossRef]
31. Hernáez, P.; Souza-Filho, J.F. A new species of the callianassid ghost shrimp genus *Cheramoides* Sakai, 2011, from Brazil (Crustacea: Decapoda: Axiidea). *J. Nat. Hist.* **2025**, *59*, 241–252. [CrossRef]
32. Rapoport, E.H. *Areography: Geographical Strategies of Species*; Pergamon Press: Oxford, UK, 1982.
33. Stevens, G.C. The latitudinal gradient in geographical range: How so many species coexist in the tropics. *Am. Nat.* **1989**, *133*, 240–256. [CrossRef]
34. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2025. Available online: https://www.R-project.org/ (accessed on 1 May 2026).
35. Roy, K.; Jablonski, D.; Valentine, J.W.; Rosenberg, G. Marine latitudinal diversity gradients: Tests of causal hypotheses. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 3699–3702. [CrossRef] [PubMed]
36. Tomašových, A.; Kennedy, J.D.; Betzner, T.J.; Kuehnle, N.B.; Edie, S.; Kim, S.; Supriya, K.; White, A.E.; Rahbek, C.; Huang, S.; et al. Unifying latitudinal gradients in range size and richness across marine and terrestrial systems. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **2016**, *283*, 20153027. [CrossRef] [PubMed]
37. Menegotto, A.; Rangel, T.F. Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nat. Commun.* **2018**, *9*, 4713. [CrossRef] [PubMed]
38. Sachs, J.D. *Tropical Underdevelopment*; National Bureau of Economic Research: Cambridge, MA, USA, 2001.
39. Amano, T.; Sutherland, W.J. Four barriers to the global understanding of biodiversity conservation: Wealth, language, geographical location and security. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **2013**, *280*, 20122649. [CrossRef] [PubMed]
40. Edie, S.M.; Smits, P.D.; Jablonski, D. Probabilistic models of species discovery and biodiversity comparisons. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 3666–3671. [CrossRef] [PubMed]
41. Diniz-Filho, J.A.F.; Bini, L.M. Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Glob. Ecol. Biogeogr.* **2005**, *14*, 177–185. [CrossRef]
42. Anger, K. *The Biology of Decapod Crustacean Larvae*; A.A. Balkema Publishers: Leiden, The Netherlands, 2001; Volume 14.
43. Paula, J.; Nogueira Mendes, R.; Paci, S.; McLaughlin, P.; Gherardi, F.; Emmerson, W. Combined effects of temperature and salinity on the larval development of the estuarine mud prawn *Upogebia africana* (Crustacea, Thalassinidea). *Hydrobiologia* **2001**, *449*, 141–148. [CrossRef]
44. Faleiro, F.; Paula, J.; Narciso, L. Hot and salty: The temperature and salinity preferences of a temperate estuarine shrimp larva, *Upogebia pusilla* (Decapoda: Thalassinidea). *Hydrobiologia* **2012**, *691*, 89–95. [CrossRef]
45. Tosetto, E.G.; Bertrand, A.; Neumann-Leitão, S.; Júnior, M.N. The Amazon River plume, a barrier to animal dispersal in the Western Tropical Atlantic. *Sci. Rep.* **2022**, *12*, 537. [CrossRef] [PubMed]
46. Rohde, K. Latitudinal gradients in species diversity and Rapoport's rule revisited: A review of recent work and what can parasites teach us about the causes of the gradients? *Ecography* **1999**, *22*, 593–613. [CrossRef]

47. Kang, Y.; Pan, D.; Bai, Y.; He, X.; Chen, X.; Chen, C.-T.-A.; Wang, D. Areas of the global major river plumes. *Acta Oceanol. Sin.* **2013**, *32*, 79–88. [CrossRef]
48. Goes, J.I.; do Rosario Gomes, H.; Chekalyuk, A.M.; Carpenter, E.J.; Montoya, J.P.; Coles, V.J.; Yager, P.L.; Berelson, W.M.; Capone, D.G.; Foster, R.A.; et al. Influence of the Amazon River discharge on the biogeography of phytoplankton communities in the western tropical north Atlantic. *Prog. Oceanogr.* **2014**, *120*, 29–40. [CrossRef]
49. Breiman, L. Random forests. *Mach. Learn.* **2001**, *45*, 5–32. [CrossRef]
50. Liaw, A.; Wiener, M. Classification and regression by random Forest. *R News* **2002**, *2*, 18–22.
51. Powell, M.G.; Beresford, V.P.; Colaianne, B.A. The latitudinal position of peak marine diversity in living and fossil biotas. *J. Biogeogr.* **2012**, *39*, 1687–1694. [CrossRef]
52. Assis, J.; Tyberghein, L.; Bosch, S.; Verbruggen, H.; Serrão, E.A.; de Clerck, O. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* **2018**, *27*, 277–284. [CrossRef]
53. Tittensor, D.P.; Mora, C.; Jetz, W.; Lotze, H.K.; Ricard, D.; Berghe, E.V.; Worm, B. Global patterns and predictors of marine biodiversity across taxa. *Nature* **2010**, *466*, 1098–1101. [CrossRef] [PubMed]
54. Naimi, B.; Hamm, N.A.; Groen, T.A.; Skidmore, A.K.; Toxopeus, A.G. Where is positional uncertainty a problem for species distribution modelling? *Ecography* **2014**, *37*, 191–203. [CrossRef]
55. Robles, R.; Tudge, C.C.; Dworschak, P.C.; Poore, G.C.B.; Felder, D.L. Molecular phylogeny of the Thalassinidea based on nuclear and mitochondrial genes. In *Crustacean Issues 18: Decapod Crustacean Phylogenetics*; Martin, J.W., Crandall, K.A., Felder, D.L., Eds.; CRC Press/Taylor & Francis: Boca Raton, FL, USA, 2009; pp. 309–326.
56. Greenwell, B.M. pdp: An R package for constructing partial dependence plots. *R J.* **2017**, *9*, 421–436. [CrossRef]
57. Pontarp, M.; Bunnefeld, L.; Cabral, J.S.; Etienne, R.S.; Fritz, S.A.; Gillespie, R.; Graham, C.H.; Hagen, O.; Hartig, F.; Huang, S.; et al. The latitudinal diversity gradient: Novel understanding through mechanistic eco-evolutionary models. *Trends Ecol. Evol.* **2019**, *34*, 211–233. [CrossRef]
58. Tomašových, A.; Jablonski, D.; Berke, S.K.; Krug, A.Z.; Valentine, J.W. Nonlinear thermal gradients shape broad-scale patterns in geographic range size and can reverse Rapoport's rule. *Glob. Ecol. Biogeogr.* **2015**, *24*, 157–167. [CrossRef]
59. Dworschak, P.C. Global diversity in the Thalassinidea (Decapoda). *J. Crustac. Biol.* **2000**, *20*, 238–245. [CrossRef]
60. Chaudhary, C.; Saeedi, H.; Costello, M.J. Bimodality of latitudinal gradients in marine species richness. *Trends Ecol. Evol.* **2016**, *31*, 670–676. [CrossRef] [PubMed]
61. Levinton, J.; Mackie, J. Latitudinal diversity relationships of fiddler crabs: Biogeographic differences united by temperature. *Glob. Ecol. Biogeogr.* **2013**, *22*, 1050–1059. [CrossRef]
62. Dworschak, P.C. Global diversity in the Thalassinidea (Decapoda): An update (1998–2004). *Nauplius* **2005**, *13*, 57–63.
63. Fernandez, M.O.; Marques, A.C. Diversity of diversities: A response to Chaudhary, Saeedi, and Costello. *Trends Ecol. Evol.* **2017**, *32*, 232–234. [CrossRef] [PubMed]
64. Yasuhara, M.; Hunt, G.; Cronin, T.M.; Okahashi, H. Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 21717–21720. [CrossRef] [PubMed]

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