



Unraveling global species richness patterns of the Lysmatidae family: a multi-scale and multi-hypothesis ecological approach

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ABSTRACT: While diversity gradients are well-explored in macroecology, factors shaping species richness at broad scales remain debated. We investigated the species richness of the decapod family Lysmatidae across 4 spatial scales: realm, province, ecoregion, and local ($2^\circ \times 2^\circ$ grid cells). We tested 4 ecological hypotheses: physiological stress (PSH), resource availability (RAH), habitat heterogeneity (HHH), and anthropogenic impact (AIH). Occurrence data (52 Lysmatidae species) and environmental variables (salinity, temperature, primary productivity, bathymetry, coral richness, anthropogenic impact index) were obtained from online databases and literature. Fifteen regression models, incorporating spatial filters, were tested to assess the hypotheses. The highest Lysmatidae species richness occurred in the Tropical Atlantic and Central Indo-Pacific realms. Richness varied with scale, with the highest values in the transition between the tropical and subtropical zones. Bathymetry was associated with Lysmatidae richness across all scales, especially at local and ecoregional scales, while coral richness was related to province and realm scales. HHH explained Lysmatidae richness patterns at the realm scale. Variables related to PSH and AIH were associated with richness at the ecoregion and province scales. Our study emphasized the importance of scale in biodiversity research, influencing richness patterns in Lysmatidae, and pointed to bathymetry, coral richness, and temperature range as the main drivers of richness. As this study showed a relationship between Lysmatidae richness, coral richness, and temperature at 3 spatial scales, this family may be susceptible to the effects of climate change, such as tropicalization of subtropical zones and defaunation of tropical ecosystems, including coral reefs.

KEY WORDS: Caridea macroecology · Decapod diversity · Biogeographical patterns · Geographical distribution · *Lysmata* · Cleaner shrimp

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1. INTRODUCTION

Contemporary studies in evolution, conservation, and ecology are aimed at comprehending global patterns of species richness and the underlying forces shaping them (Tittensor et al. 2010). The fluctuation in species richness concerning the observed scale has been a topic of debate (Chase et al. 2019). Globally, both current and historical anthropogenic factors have contributed to the extinction of numerous taxa

(Barnosky et al. 2011, Pimm et al. 2014, McCauley et al. 2015), resulting in a worldwide decrease in species richness, although this decline is not consistently evident at regional or local scales (Primack et al. 2018).

In the marine environment, various ecological hypotheses have been proposed to elucidate diversity gradients (Pianka 1966, Brown & Gibson 1983, Okolodkov 2010). Among the principal hypotheses are the kinetic energy hypothesis or temperature hypothesis, which correlates metabolic rates with higher temperatures,

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consequently promoting greater levels of speciation and biodiversity (Rohde 1992, Allen et al. 2007); the productivity–richness hypothesis, which posits that high richness is conditioned by high rates of primary productivity (Gaston 2000, Evans et al. 2005); and the environmental stress hypothesis, which proposes an inversely proportional relationship between richness and environmental stress (Keeling et al. 2010).

Among the numerous alternative hypotheses, there is a nearly unanimous consensus on the necessity of examining the relationship between richness and temperature variation. As per Janzen (1967), a reduction in seasonal temperature extremes in the tropics would facilitate the evolution of species with low thermal tolerance. These species would structure themselves into narrower ecological niches, enabling a greater number of species to coexist in the tropical region. In addition to temperature, rainfall variation, such as dry and wet seasons, can alter turbidity and nutrient input in coastal regions (McClanahan 1988). Therefore, the relationship between niche breadth (and consequently richness) and latitude hinges on the environmental factors considered, including productivity, temperature, and salinity, among others (Vázquez & Stevens 2004).

In addition to these hypotheses traditionally studied in ecology, 2 other hypotheses have been investigated from the perspective of climate change and anthropogenic alterations (Luypaert et al. 2020). The climatic stability hypothesis suggests a directly proportional relationship between environmental stability and diversity (Fraser & Currie 1996), while the habitat availability hypothesis supports the positive effect of habitat availability on diversity (Etnoyer et al. 2004, Worm et al. 2005). These hypotheses have been extensively studied due to the various impacts on marine systems, including the presence of different types of pollutants, the expansion of invasive species distributions, and ocean warming and acidification processes. These factors have culminated in the widespread bleaching of coral reef areas and the over-exploitation of marine species across multiple fishing levels (Luypaert et al. 2020).

Human activities can also disrupt the distribution processes of marine species, acting as stressors for communities (Giraldes et al. 2021). They have the potential to modify marine food webs and establish new ecosystems with diversities different from those that existed before anthropogenic actions intervened (Jackson et al. 2001, Pereira et al. 2018, Giraldes et al. 2021). Examples of significant impacts on marine ecosystems include the removal of predators from the food chain due to fishing activities (Boudreau &

Worm 2012), modification of benthic cover in reef environments caused by tourism, and the increasing urbanization of coastal areas (Dwyer & Edwards 2000).

To understand the factors contributing to the emergence of species richness gradients in the marine environment, and recognizing that these factors may vary among different taxa (Tittensor et al. 2010), we focused on the monophyletic clade formed by shrimps of the genus *Lysmata* (51 described species), *Lysmatella* (1 described species), *Exhippolysmata* (4 described species), and *Mimocaris* (1 described species) (Infraorder: Caridea; Family: Lysmatidae) (De Grave & Fransen 2011, Baeza & Prakash 2019, Aguilar et al. 2022). This family Lysmatidae demonstrates ecological relevance by exhibiting a complex and uncommon sexual reproductive system, characterized by simultaneous protandry (Baeza et al. 2009, Baeza 2010a,b), adopting different lifestyles (free-living, obligatory and/or facultative symbiosis, occurrence in pairs, and aggregations), and performing ecosystem functions such as cleaning fish, corals, and anemones (Bauer 2000, Baeza & Bauer 2004, Baeza 2006, 2007, 2008, 2013, Baeza et al. 2009, Baeza & Prakash 2019, Aguilar et al. 2022).

Furthermore, the group, in addition to facing fishing pressure from the aquarium trade market, has representatives registered as invasive species in various locations (Calado et al. 2003, Calado 2009, Aguilar et al. 2022, Guéron et al. 2022). Recently, a study on *Lysmata uncicornis* revealed an expansion of the distribution of this species towards subtropical regions of the Atlantic Ocean (González-Ortegón et al. 2020), indicating the possibility of an initial process of tropicalization in these areas.

Finally, the Lysmatidae are widely distributed across the planet (Calado et al. 2003, Rhyne & Lin 2006, Anker et al. 2009, Baeza et al. 2009, Calado 2009, Baeza 2010, Prakash & Baeza 2017, De Grave & Anker 2018), occupying both tropical and subtropical regions (De Grave & Anker 2018, Giraldes et al. 2018) and various habitats such as rocky environments, coral reefs, and seagrass beds (Bauer & Holt 1998, Rhyne & Lin 2006). They thrive at depths ranging from intertidal zones to about 300 m, as exemplified by *L. philippinensis* (Chace 1997, Rhyne & Lin 2006).

Given the diverse pressures impacting the marine environment during the Anthropocene (Luypaert et al. 2020), and the remarkable diversity of lifestyles exhibited by the Lysmatidae, characterized by a range of ecological, physiological, and morphological adaptations (Bauer 2000, Baeza & Bauer 2004, Baeza 2006, 2007, 2008, 2013, Baeza et al. 2009, Baeza & Prakash

2019, Aguilar et al. 2022), we suggest that investigating the richness patterns of this clade provides insights into the impacts of natural environmental variables (e.g. productivity, historical factors, salinity) as well as the continuing anthropogenic influence on marine ecosystems.

Therefore, in this study, we aimed to evaluate the global distribution of Lysmatidae species richness and determine whether various ecological hypotheses could influence Lysmatidae distribution at 4 scales: realm, province, ecoregion (Spalding et al. 2008), and local ($2^\circ \times 2^\circ$ grid cells). Based on the physiological stress hypothesis (PSH), we investigated whether high variations in temperature and salinity could lead to a reduction in Lysmatidae richness at both local and regional scales, thereby reducing their dispersal capacity (Janzen 1967). Under the habitat heterogeneity hypothesis (HHH), we explored the relationship between coral richness, bathymetry, and Lysmatidae species richness on a global scale. We hypothesized that habitat availability would enable resource use diversification and, consequently, speciation through niche specialization (Bazzaz 1975, Tews et al. 2004, Sanciangco et al. 2013). Additionally, we examined the resource availability hypothesis (RAH) to determine whether primary productivity was positively correlated with richness, promoting greater species coexistence (Hawkins et al. 2003) at local and regional scales. Lastly, we assessed whether the anthropogenic impact hypothesis (AIH) could be supported by observing lower species richness in areas with higher anthropogenic impact (Torres-Romero & Olalla-Tárraga 2015), potentially associated with the loss of specialist species and subsequent biotic homogenization, particularly at broader scales (McKinney & Lockwood 1999, Gossner et al. 2016, Chase et al. 2019).

2. MATERIALS AND METHODS

2.1. Data acquisition and processing

We conducted a comprehensive survey of occurrence points for Lysmatidae species, utilizing literature reviews and data from the Global Biodiversity Information Facility (GBIF, www.gbif.org, as of 20 November 2023) and the Ocean Biodiversity Information System (OBIS; <https://obis.org/>, as of 20 November 2023). We considered occurrences recorded between 1899 and 2023. To work with this extensive temporal scale, we assume the perspective of niche conservatism, where sister species, such as those studied in this investigation, tend to conserve their

niches over thousands of years of independent evolution, with speciation occurring at geographic scales and ecological modifications arising later (Peterson et al. 1999)

The family Lysmatidae has 58 valid species, according to the World Register of Marine Species (WoRMS) (WoRMS Editorial Board 2024 and the phylogeny of Aguilar et al. 2022). We also included *Lysmata* sp. AUS1 and *Lysmata* sp. AUS2 (belonging to the *Lysmata rauli* complex, as proposed by Guéron et al. 2022), that have not yet been formally described. This inclusion was possible because the occurrences of *Lysmata* sp. AUS1 and *Lysmata* sp. AUS2 found on the Australian coast could be other occurrences of the *L. rauli* complex. However, there is no distinction among occurrence records in GBIF; populations were classified *a posteriori*. Although we know that *Lysmata* sp. AUS1 and *Lysmata* sp. AUS2 are distinct species, we will treat them as a species complex, which we refer to as *Lysmata* sp. AUS. Neither *Lysmata* sp. AUS1 nor *Lysmata* sp. AUS2 have been formally described and neither are listed in WoRMS. Furthermore, these data are significant, as they contribute to representing the diversity already identified within the *L. rauli* complex. In addition, all 4 species of the genus *Exhippolysmata* were considered, as were *Lysmatela prima* and *Mimocaris heterocarpoides*.

From the 59 species of the family, 4 species of the genus *Lysmata* (*L. kempi*, *L. leptodactylus*, *L. splendida*, and *L. stenolepis*) were excluded due to insufficient data in the databases or because the species description papers lacked precise longitude and latitude data (Ahyong et al. 2024). Additionally, 2 species (*L. baueri* and *L. durbanensis*) were excluded during the data occurrence processing, because it was not possible to perform their spatial adjustment to the resolution of the environmental variables ($2^\circ \times 2^\circ$ grid cells). The genus *Ligur*, composed of a single species (*L. ensiferus*), was not considered in this work, since it shows an uncertain basal position in the 2 phylogenetic trees (maximum likelihood, Bayesian inference) proposed by Aguilar et al. (2022), which suggests that the family Lysmatidae is a paraphyletic group (for more details, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m748p083_supp.xlsx).

Despite evidence suggesting new synonymies (Ashrafi et al. 2021, Aguilar et al. 2022), there is still no consensus in the literature regarding them (e.g. *Lysmata kuekenthali* and *L. hochi*, Ashrafi et al. 2021; and *L. dispar* and *L. lipkei*, Aguilar et al. 2022). Therefore, distinct species were considered here in accordance with the WoRMS database (Ahyong et al. 2024). There are still some complexes of cryptic species

awaiting further detailed studies, including the *L. wurdemanni* complex sensu Baeza & Prakash (2019), the *L. vittata* complex (Aguilar et al. 2022, Guéron et al. 2022), and the *L. rauli* complex (Guéron et al. 2022). In this study, the *L. wurdemanni* complex was treated as a single species, as the putative species in the complex have not been formally described (Baeza & Prakash 2019). The occurrences of *L. vittata* from the Red Sea and Mediterranean Sea were reevaluated and removed due to evidence suggesting that they are specimens of *L. rauli* sensu lato (Aguilar et al. 2022, Guéron et al. 2022).

In addition to all the caution already mentioned with the treatment of occurrences and which species would be used in this study, we also considered the possibility that many records represent cases of Lysmatidae species invasions. Although we are aware of cases of invasions, such as *L. lipkei* and *L. vittata* in the western Atlantic (Almeida et al. 2021, Aguilar et al. 2022), our study focused on assessing species distributions without distinguishing between native and non-native occurrences. Our aim was to investigate the environmental factors that facilitate species co-occurrence within the family, encompassing both native and invasive species.

All occurrences underwent rigorous standardization to ensure consistency with predictor variables (5 arc-min resolution) using the Bio-Oracle database (<http://bio-oracle.org/>, accessed on 25 May 2020) (Tyberghein et al. 2012, Assis et al. 2018) (Table S1). We considered the spatial structure of the data and the inherent spatial autocorrelation, employing spatial filtering through linear eigenvectors. Instead of analyzing each environmental variable separately in a linear regression, we chose to work with 2 variables derived from the spatial relationships of the data (Diniz-Filho & Bini 2005). To mitigate potential sampling biases, we removed duplicate occurrences or those with ambiguous georeferenced records (instances where more than 1 occurrence was recorded in the same pixel) (Fourcade 2016, de Andrade et al. 2020). Following this, we refined species occurrences by randomly selecting 1 instance within each grid cell at a resolution double that of the environmental variables (Velazco et al. 2019).

Subsequently, occurrences were plotted and overlaid to determine richness at 4 distinct spatial scales: realm, province, ecoregion, and map grid cell ($2^\circ \times 2^\circ$ grid cell resolution, equivalent to $\sim 220 \times 220$ km²). The spatial delin-

eation of realm (10), province (48), and ecoregion (115) was informed by Spalding et al. (2008) (Table S1). The processing of occurrences at each scale was executed using RStudio (R version 4.3.2; R Core Team 2023).

To elucidate the factors influencing the richness distribution of the Lysmatidae, we selected 8 variables based on the scientific literature, which formed the hypotheses tested in this study. These variables included annual temperature (mean and range), annual salinity (mean and range), bathymetry and primary productivity (mean), obtained from the Bio-Oracle database (<http://bio-oracle.org/>, accessed on 25 May 2020). Additionally, coral richness and the anthropogenic impact index were obtained from the IUCN Red List (www.iucnredlist.org, accessed on 16 June 2022) and from the National Center of Ecological Analysis and Synthesis (NCEAS; <https://www.nceas.ucsb.edu/>), respectively. Although annual salinity (range), annual dissolved oxygen (range), current velocity (range), bathymetry, and luminosity (range) were considered, they exhibited collinearity problems, with correlation values less than 0.70 and variance inflation factors (VIFs) less than 5.0 (Fig. S1, Table S2).

2.2. Hypotheses

Four hypotheses were proposed to elucidate the richness patterns of Lysmatidae: PSH, HHH, RAH, and AIH (Table 1). In the PSH, we used temperature (range and mean, °C) and salinity (mean, PSS) as indicators of environmental stress (Fig. 1A,B). In the HHH, we used coral richness and bathymetry as variables to represent habitat heterogeneity (Fig. 1C,D). Coral richness data were obtained from distribution maps for 561 reef-building coral species from the IUCN Red List. Subsequently, these maps were overlaid on a grid with cells of $2^\circ \times 2^\circ$ resolution (approx-

Table 1. Description of variables evaluated for the studied hypotheses. PSH: physiological stress hypothesis; RAH: resource availability hypothesis; HHH: habitat heterogeneity hypothesis; AIH: anthropogenic impact hypothesis

Variables	PSH	RAH	HHH	AIH
Anthropogenic impact index	X			X
Bathymetry (m)			X	X
Coral richness			X	
Primary productivity mean (g m ⁻³ d ⁻¹)		X	X	
Annual salinity mean (PSS)	X			
Annual salinity range (PSS)	X			
Annual temperature mean (°C)	X			
Annual temperature range (°C)	X			

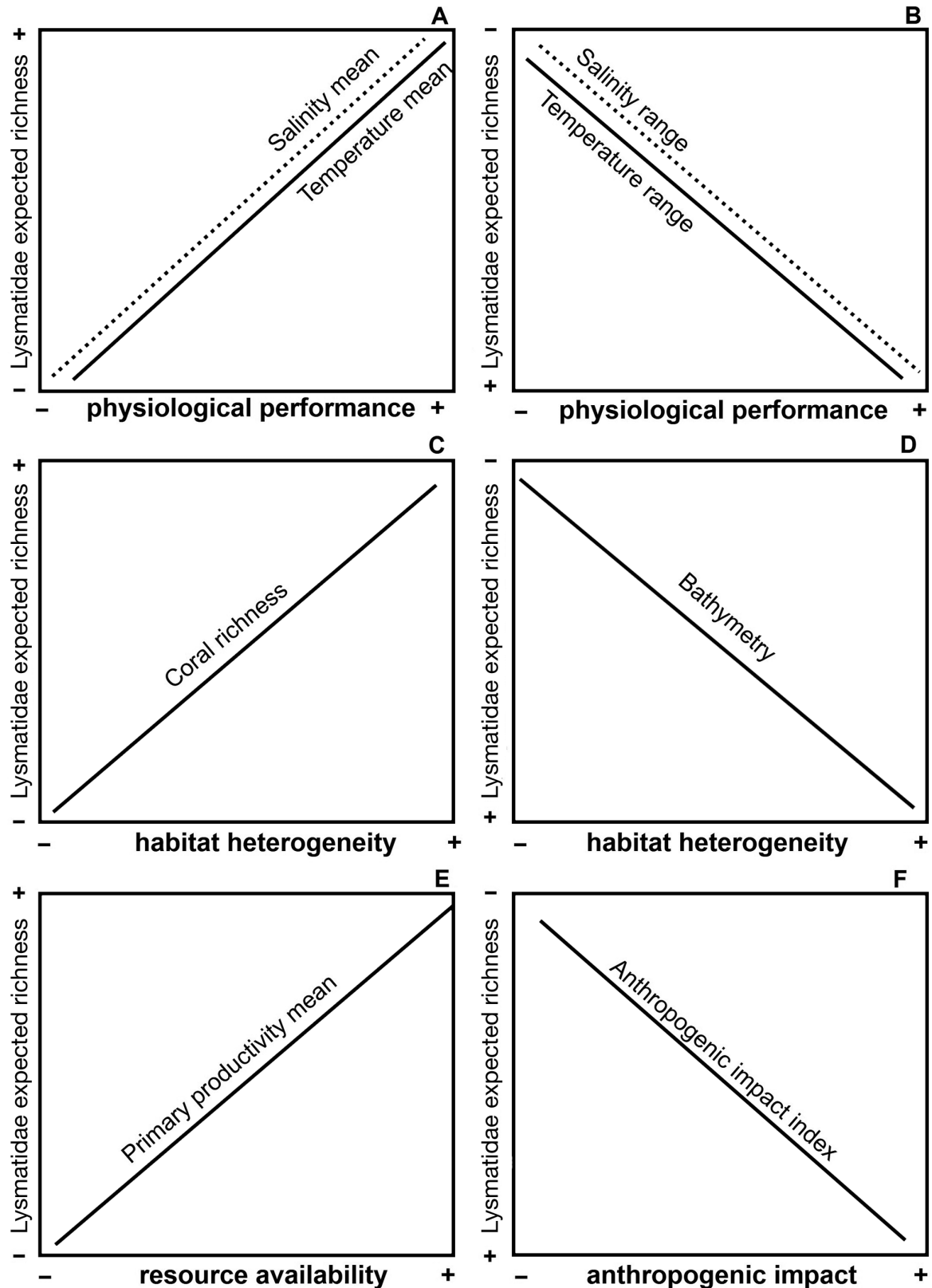


Fig. 1. Formulated hypotheses, illustrating the expected effect of each variable on the species richness of the family Lysmatidae. Physiological stress hypothesis: effect of the variables (A) mean temperature and mean salinity and (B) temperature range and salinity range. Habitat heterogeneity hypothesis: effect of (C) coral richness and (D) bathymetry. Resource availability hypothesis: effect of (E) mean primary productivity. Anthropogenic impact hypothesis: effect of (F) anthropogenic impact

imately 220×220 km at the Equator) by aggregating the overlapping distribution ranges within each grid cell. The processing of these maps was conducted using the 'raster' package (Hijmans et al. 2021) in RStudio (R version 4.3.2). In the RAH, we used the mean primary productivity as an indicator of resource availability (Fig. 1E).

Lastly, we assessed the AIH through an anthropogenic impact index (Fig. 1F), a composite of 19 anthropogenic factors contributing to ecological changes in the oceans. This index evaluated the effect of various stressors on the marine environment, including different levels of fishing (from artisanal to high-impact demersal), shipping activities, presence of oil platforms, direct human impact, various sources of pollution, invasive species, ocean acidification, sea surface temperature, sea level rise, and UV radiation incidence (Halpern et al. 2015). The cumulative impact of these stressors was based on assumptions of linear and additive responses within natural systems. However, it is important to consider that marine ecosystems may exhibit threshold responses to intense and cumulative stressors, resulting in nonlinear cumulative impact responses within ecological relationships (Halpern et al. 2015). Such responses are common but difficult to predict. Therefore, the index provides an overview of how environmental pressures are changing over time and identifies areas where mitigation efforts are most necessary (Halpern et al. 2015).

2.3. Statistical analyses

This study was based on the assumption of an equilibrium or pseudo-equilibrium existing between the environment and observed species patterns (Lischke et al. 1998, Guisan & Zimmermann 2000). The adoption of the pseudo-equilibrium principle is justified due to its broad-scale predictive power and the lack of detailed data on the physiology and behavior of the studied species (Guisan & Zimmermann 2000, Pickett et al. 2010). Furthermore, given the limited research conducted on the Lysmatidae as a group, the principle of pseudo-equilibrium enables us to leverage the maximum available information gleaned from occurrence records amassed thus far.

To perform spatial filter analyses, we utilized the geographical coordinates (latitude and longitude) of each cell on the globe to construct a paired matrix of geographical distances between cells (Diniz-Filho et al. 2003). This distance provides weight to short-distance effects following the filtering process (Diniz-Filho et al. 2003). The association between eigenvec-

tors and positive eigenvalues of the matrix represents the spatial relationship between globe cells at different spatial scales (Diniz-Filho et al. 2003). The geometry of the geographic area under study allows their incorporation into a multiple regression approach, while considering spatial autocorrelation and enabling unbiased prediction of regression parameters (Diniz-Filho et al. 2003).

To test the different hypotheses, we constructed 15 regression models using the spatial eigenvector filtering method (Murakami 2022). This approach removes the bias of spatial autocorrelation in the residuals of general linear model (GLM) regression, thereby enhancing the reliability of estimating the effects of each variable, as the filters represent distinct and independent propositions of how map cells are geographically related or connected to each other (Diniz-Filho & Bini 2005). The filters are expressed as new variables derived from geographical distances and the spatial relationships between cells (Diniz-Filho & Bini 2005).

The selection of the best model was based on Akaike's information criterion (AIC). According to this criterion, the model that best explains the studied phenomenon is the one with $\Delta AIC = 0$, as it represents the least loss of information when the model is used to approximate the total reality (Johnson & Omland 2004, Burnham et al. 2011). After adjusting each model to the data and calculating the AIC score, differences in these scores between each model and the best model were computed (the best model in the set has the minimum AIC score: $\Delta i = AIC_i - AIC_{min}$) (Johnson & Omland 2004). All models with $\Delta AIC < 4$ were considered to have substantial support (Burnham et al. 2011). Akaike weights are additive and can be summed to provide a set of trustworthy models with a specific probability that the best-fitting model is contained within the confidence set (Johnson & Omland 2004).

Upon evaluating the models based on the AIC, we proceeded to assess the performance of the top-ranking models by examining their goodness of fit, while acknowledging the finite nature of the data and recognizing that models serve as approximations of reality (Burnham & Anderson 2004). All statistical analyses were executed using RStudio (R version 4.3.2).

3. RESULTS

A total of 4125 data points were collected, with 243 sourced from literature reviews. Following data screening, 966 occurrence points were selected for analysis. The highest richness of Lysmatidae was present in the

transition areas between tropical and subtropical regions in both hemispheres (Fig. 2). The distribution of Lysmatidae richness across 4 scales — realm, province, ecoregion, and local ($2^\circ \times 2^\circ$ grid cell) — reveals a circumtropical dispersion (Fig. 3).

At the local scale (cell), the highest richness is concentrated in the southern portion of the Gulf of Mexico (7 species) and on the west part of the Florida (USA) coast, reaching a peak of 10 species (Fig. 3A). At the ecoregion scale, the northern region of the Gulf of Mexico (9–12 species) and the southwestern Caribbean (12–15 species) display the highest richness values in the Atlantic. In the Indo-Pacific, the Eastern Philippines ecoregion features scattered areas where species richness reaches its peak (12 species) (Fig. 3B).

At the province scale, we observed that the highest richness is concentrated in the tropical region of the North Atlantic (Tropical Northwestern Atlantic), but it extends into a transition area in the subtropical region of the Warm Temperate Northwestern Atlantic province. Intermediate values of richness were observed in the South Atlantic (Tropical Southwestern Atlantic; richness range: 14–19 species). In the Pacific Ocean, we observed several patches of richness, with peaks reaching 10–14 species in the Western

Coral Triangle province (Fig. 3C). On the realm scale, we observed 2 peaks of Lysmatidae richness in tropical regions, one in the Atlantic Ocean and the other in the Eastern Pacific (Fig. 3D). Subtropical regions of the northern Atlantic Ocean (Temperate Northern Atlantic realm), and tropical regions of the Indo-Pacific (Western Indo-Pacific realm) presented intermediate values of Lysmatidae richness (Fig. 3D).

Among the hypotheses explored to elucidate the distribution patterns of Lysmatidae richness (PSH, RAH, HHH, and AIH), only at the realm scale was the best model composed of a single hypothesis (Fig. 4). The best models ($\Delta AIC = 0$) and the contribution of the studied variables varied across scales. At the realm scale, the best model was HHH (adjusted $R^2 = 0.87$, Moran's $I = 0.34$, spatial effects residuals, $SE = 0.89$), where coral richness exhibited the highest contribution and a positive relationship with richness (estimates = 0.08, $t = 2.75$, $p < 0.01$), followed by bathymetry, showing an equally significant relationship to Lysmatidae richness (estimates = 0.06, $t = 2.74$, $p < 0.01$). At the province scale, the best model was PSH+RAH+HHH+AIH (adjusted $R^2 = 0.92$, Moran's $I = 0.36$, $SE = 0.96$), with bathymetry (estimates = 0.08, $t = 2.63$, $p = 0.01$) showing the highest contribution to the model, followed by coral richness (esti-

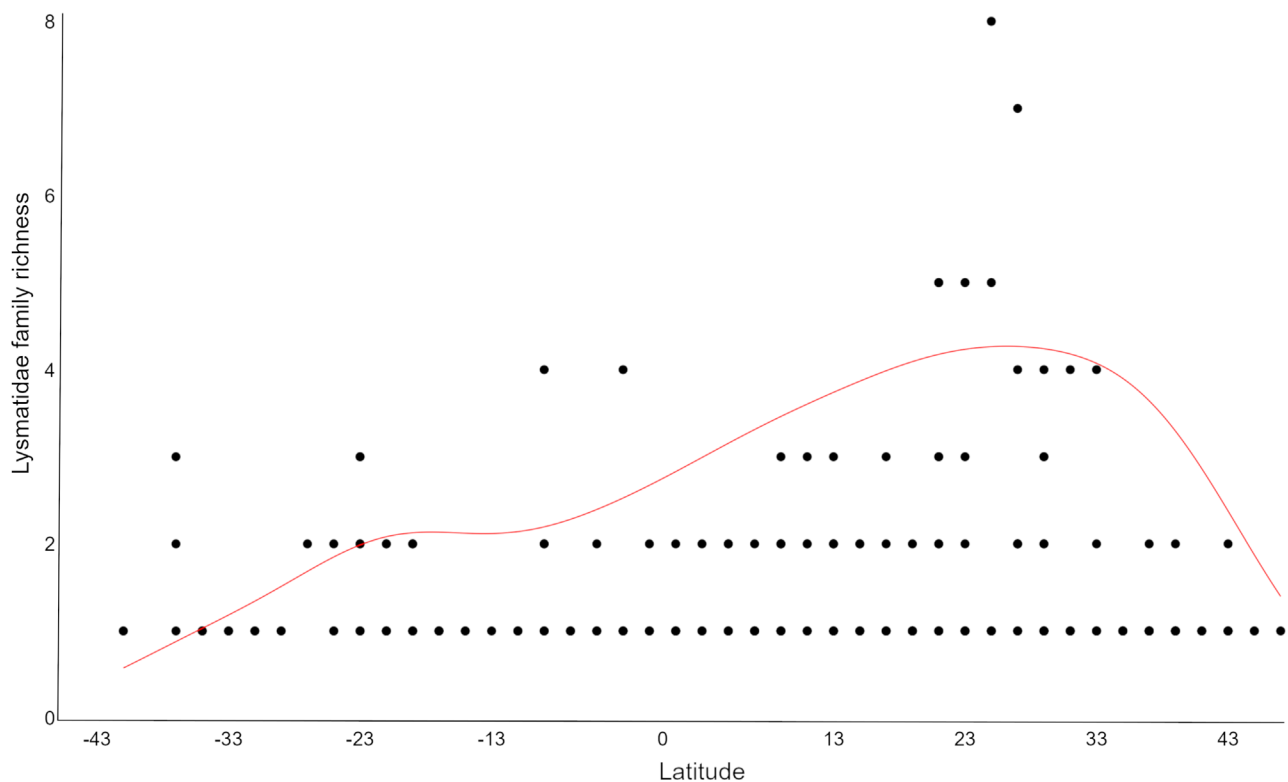


Fig. 2. Species richness of the Lysmatidae across latitudes. Black dots = species richness values of the Lysmatidae family on a local scale

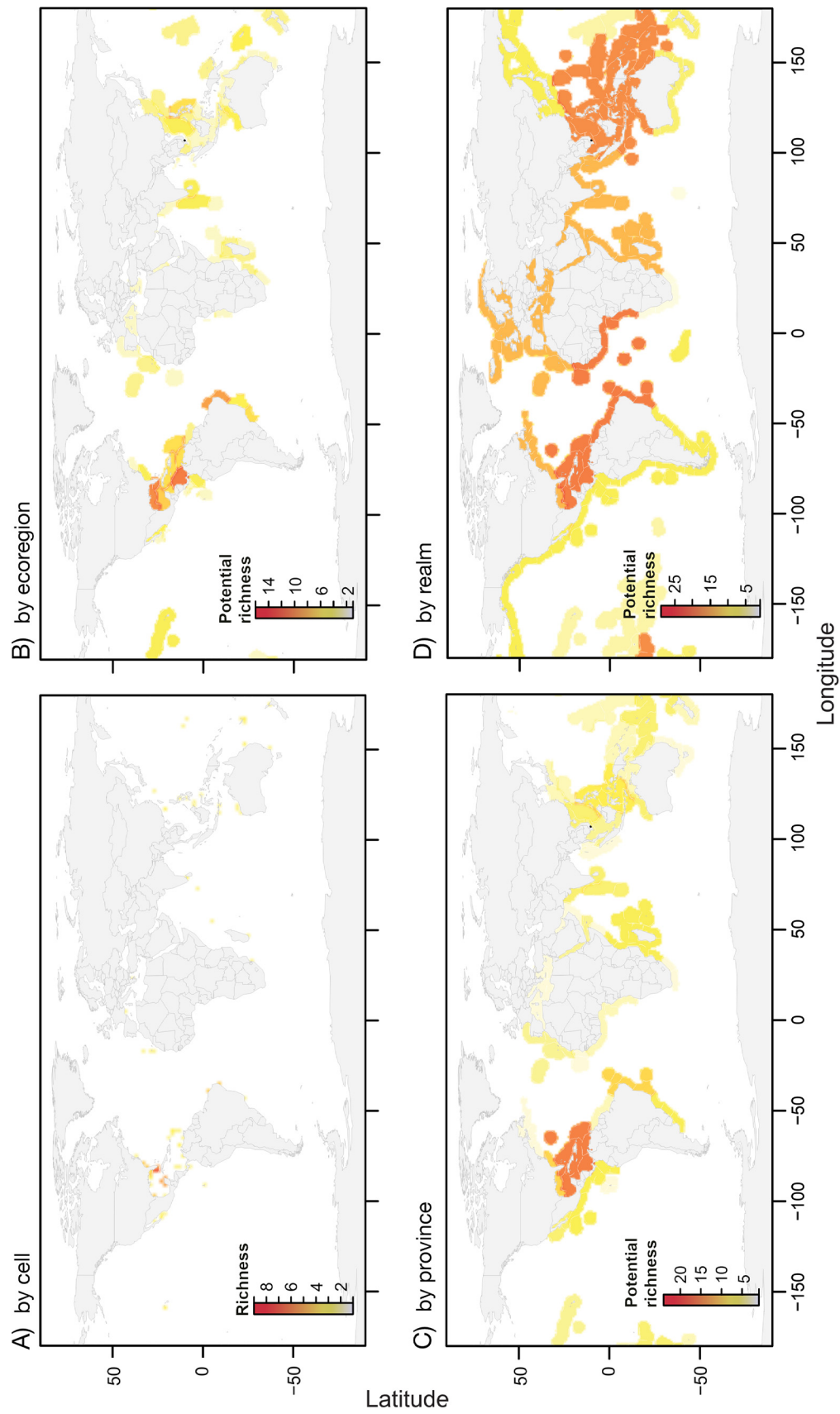


Fig. 3. Distribution of Lysmatidae species richness, organized by spatial scales. Colors represent different species richness values in each panel. Numbers indicate (A) the species richness found at the local scale (per cell) (maximum value = 10); (B) the potential species richness for the ecoregion scale (maximum value = 15); (C) the potential species richness for the province scale (maximum value = 24); and (D) the potential species richness for the realm scale (maximum value = 29)

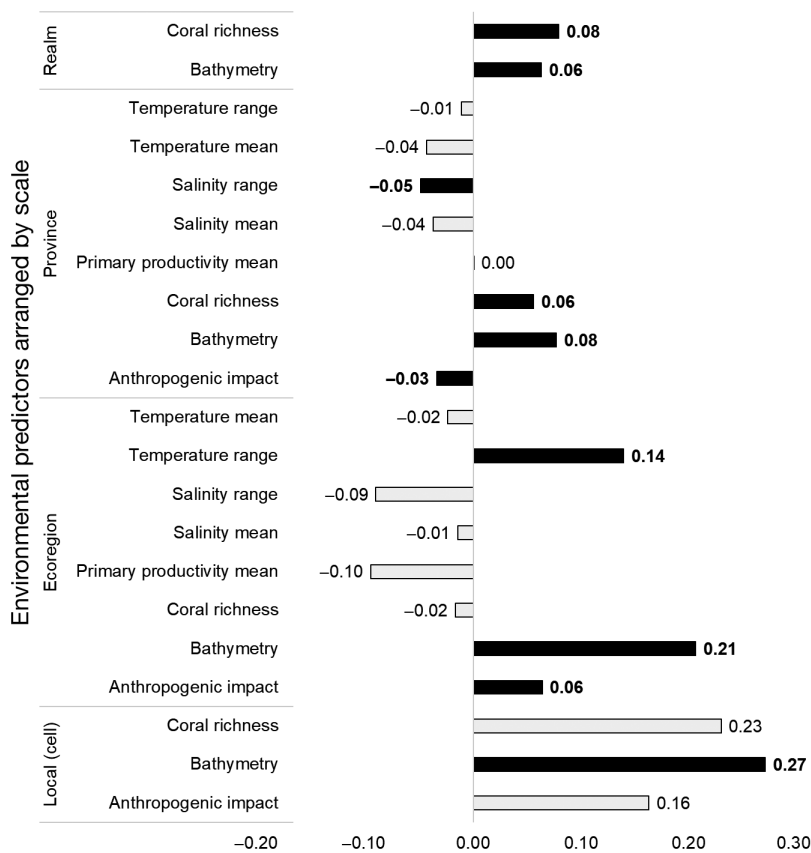


Fig. 4. Slopes of regression models arranged by scale. **Bold** values (black bars) indicate $p < 0.05$

mates = 0.06, $t = 2.31$, $p = 0.02$), salinity range (estimates = -0.05 , $t = -2.18$, $p = 0.03$), and anthropogenic impact (estimates = -0.03 , $t = -2.54$, $p = 0.01$). At the ecoregional scale, the best model was PSH+RAH+HHH+AIH (adjusted $R^2 = 0.66$, Moran's $I = 0.31$, $SE = 0.84$), with bathymetry (estimates = 0.21, $t = 3.22$, $p < 0.01$), temperature range (estimates = 0.14, $t = 2.67$, $p < 0.01$), and anthropogenic impact (estimates = 0.06, $t = 1.97$, $p = 0.05$) displaying a positive relationship with richness and making the most substantial contributions to the model. Finally, at the local scale ($2^\circ \times 2^\circ$ grid cells), HHH+AIH was identified as the optimal model (adjusted $R^2 = 0.25$, Moran's $I = 0.68$, $SE = 0.64$), with bathymetry exhibiting the highest contribution and a positive relationship with richness (estimates = 0.27, $t = 2.68$, $p < 0.01$).

4. DISCUSSION

The models employed in this study effectively elucidated variations in richness within the group, explaining a substantial proportion ranging from 25 to 92%, as depicted in the presented scales (Table 2).

This explained percentage holds significance when compared to other studies investigating richness patterns in marine animals, where R^2 values fluctuated between 15 and 89% (Tittensor et al. 2010, Parravicini et al. 2013, Martinez et al. 2021). It is noteworthy that in comparison to the studies cited here, those demonstrating the highest percentages in explaining richness distribution considered not only environmental factors but also historical and phylogenetic factors. This affirms the relevance of the analyzed environmental factors in predicting the clade richness, as revealed by our results.

Our findings substantiate inter- and intra-regional disparities in species diversity patterns in tropical marine environments, as observed by Frey & Vermeij (2008). We observed the highest richness of the Lysmatidae in the region between the Caribbean Sea and the Gulf of Mexico, aligning with the same hemispheric asymmetry noted by Chaudhary et al. (2016) for marine species. In contrast to the suggestion by Tittensor et al. (2010) that coastal

species tend to be disproportionately concentrated in Southeast Asia, the Lysmatidae exhibit higher richness in the Caribbean and Gulf of Mexico region, despite significant richness values also being present in the Philippines region.

Although the Tropical Atlantic and Central Indo-Pacific realms have the same number of species, richness is distributed more evenly in the Central Indo-Pacific, with ecoregions showing maximum values of 9 species. In the Tropical Atlantic, however, we observed richness peaks in 3 ecoregions: the northern Gulf of Mexico, Floridian and southwestern Caribbean (ranging from 9 to 15 species). This fact may be related to a biogeographic pattern from the Indian Ocean and Western Pacific, where there is a decreasing gradient in the number of species as we move away from the Coral Triangle region in any direction (Briggs 1999, 2005). Moreover, the fact that Caribbean coral reefs have a significantly smaller area than those present in the Coral Triangle region (Briggs 2005) and are close to a major barrier such as the Amazon River plume (Giachini Tosetto et al. 2022) may contribute to the concentration of species diversity in the tropical ecoregions of the western Atlantic.

Table 2. Model ranking according to Akaike's information criterion (AIC). Models in **bold**: $\Delta AIC = 0$. BIC: Bayesian information criterion. Hypothesis abbreviations as in Table 1

Scale	Model	SD	Moran's I/ $\max_{(MoranI)}$	Residual SE	Adj. R ²	logLik	AIC	ΔAIC	Rank	BIC
Local (cell)	HHH + AIH	0.64	0.68	0.87	0.25	-102.62	229.23	0.00	1	259.54
	RAH + HHH + AIH	0.63	0.70	0.87	0.25	-102.07	230.13	0.90	2	261.89
	HHH	0.63	0.55	0.87	0.21	-102.27	230.53	1.30	3	262.29
	PSH + HHH	0.66	0.72	0.87	0.24	-102.28	230.56	1.33	4	262.32
	PSH + AIH	0.50	0.54	0.87	0.24	-101.72	231.44	2.21	5	265.64
	RAH + HHH	0.61	0.56	0.87	0.24	-101.76	231.52	2.29	6	265.71
	PSH	0.50	0.45	0.88	0.23	-102.82	231.64	2.41	7	263.39
	AIH	0.50	0.45	0.90	0.19	-106.84	233.68	4.45	8	258.11
	RAH + AIH	0.50	0.45	0.91	0.18	-106.82	235.64	6.41	9	262.51
	RAH	0.51	0.37	0.91	0.18	-106.96	235.92	6.69	10	262.79
	PSH + RAH + AIH	NA	NA	0.94	0.12	-111.56	239.12	9.89	11	258.66
	PSH + RAH	NA	NA	0.95	0.10	-112.87	239.74	10.51	12	256.84
	PSH + RAH + HHH + AIH	NA	NA	0.93	0.13	-110.06	240.12	10.89	13	264.55
	PSH + RAH + HHH	NA	NA	0.95	0.11	-111.64	241.29	12.06	14	263.27
Ecoregion	PSH + RAH + HHH + AIH	0.84	0.308	0.57	0.66	-419.91	925.83	0.00	1	1106.97
	RAH + HHH + AIH	0.82	0.307	0.59	0.65	-424.18	928.36	2.54	2	1096.87
	PSH + RAH + AIH	0.83	0.311	0.59	0.65	-422.08	930.16	4.33	3	1111.30
	RAH + HHH	0.81	0.292	0.59	0.65	-426.32	930.64	4.81	4	1094.93
	PSH + RAH + HHH	0.83	0.291	0.59	0.65	-425.00	930.85	5.02	5	1099.35
	PSH + AIH	0.83	0.318	0.59	0.65	-424.50	931.00	5.17	6	1103.71
	PSH + RAH	0.83	0.296	0.59	0.65	-423.88	931.76	5.93	7	1108.69
	PSH	0.82	0.302	0.59	0.65	-426.44	932.88	7.05	8	1101.39
	PSH + HHH	0.82	0.297	0.59	0.65	-427.61	933.22	7.39	9	1097.51
	HHH + AIH	0.82	0.323	0.60	0.64	-432.61	941.21	15.39	10	1101.29
	RAH + AIH	0.81	0.302	0.60	0.64	-435.60	943.202	17.37	11	1094.86
	HHH	0.82	0.307	0.60	0.64	-434.83	943.66	17.84	12	1099.53
	RAH	0.81	0.288	0.60	0.64	-435.60	945.20	19.37	13	1101.06
	AIH	0.81	0.312	0.60	0.63	-439.38	948.77	22.94	14	1096.21
Province	PSH + RAH + HHH + AIH	0.96	0.361	0.84	0.92	-78.88	279.77	0.00	1	556.24
	RAH + HHH + AIH	0.95	0.364	0.29	0.92	-82.70	281.40	1.63	2	544.28
	PSH + HHH	0.96	0.364	0.29	0.92	-82.36	282.72	2.95	3	550.12
	PSH + RAH + HHH	0.96	0.365	0.29	0.92	-82.33	284.67	4.90	4	556.61
	RAH + HHH	0.95	0.367	0.29	0.92	-86.18	286.36	6.59	5	544.70
	HHH + AIH	0.95	0.366	0.29	0.92	-87.39	288.78	9.01	6	547.13
	RAH + AIH	0.95	0.350	0.29	0.92	-91.78	289.55	9.79	7	529.77
	HHH	0.95	0.368	0.29	0.92	-90.79	291.57	11.81	8	540.85
	PSH + AIH	0.96	0.351	0.29	0.92	-86.95	291.89	12.12	9	559.30
	PSH + RAH + AIH	0.96	0.350	0.29	0.92	-86.80	293.60	13.83	10	565.54
	AIH	0.96	0.349	0.29	0.92	-94.21	294.42	14.65	11	534.63
	PSH	0.96	0.354	0.29	0.92	-90.56	297.13	17.36	12	560.01
	RAH	0.96	0.353	0.29	0.92	-95.60	297.19	17.42	13	537.40
	PSH + RAH	0.96	0.354	0.29	0.92	-90.48	298.97	19.20	14	566.38
Realm	HHH	0.89	0.338	0.36	0.87	-270.74	661.49	0.00	3	938.93
	HHH + AIH	0.89	0.337	0.36	0.87	-270.63	663.25	1.77	10	945.32
	RAH + HHH	0.89	0.338	0.36	0.87	-270.74	663.48	1.99	8	945.55
	PSH + HHH	0.89	0.337	0.36	0.87	-268.34	664.67	3.18	6	960.61
	RAH + HHH + AIH	0.89	0.337	0.36	0.87	-270.62	665.24	3.76	13	951.93
	PSH + RAH + HHH	0.89	0.337	0.36	0.87	-268.12	666.25	4.76	11	966.81
	PSH + RAH + HHH + AIH	0.89	0.336	0.36	0.87	-268.01	668.01	6.53	14	973.20
	PSH	0.91	0.35	0.36	0.87	-274.89	675.78	14.29	1	967.09
	PSH + AIH	0.91	0.351	0.36	0.87	-274.82	677.65	16.16	7	973.59
	PSH + RAH	0.91	0.351	0.364	0.87	-274.87	677.75	16.26	5	937.69
	PSH + RAH + AIH	0.91	0.35	0.36	0.87	-274.80	679.61	18.12	12	980.17
	RAH	0.93	0.361	0.37	0.87	-279.94	681.89	20.40	2	963.96
	AIH	0.94	0.362	0.37	0.87	-280.16	682.32	20.84	4	964.39
	RAH + AIH	0.94	0.361	0.37	0.87	-279.92	683.85	22.36	9	970.54

The models supported in this study indicate that the studied variables explain the richness pattern differentially at each observed scale, confirming that the extent of a geographic area can significantly influence the derived species richness pattern (Rahbek 2005). In this study, it is evident that factors related to habitat heterogeneity are the primary predictors of Lysmatidae richness, corroborating the insights of Tittensor et al. (2010) regarding the relevance of this resource for marine organisms. At the realm scale, we observed a positive impact of coral richness and bathymetry on Lysmatidae richness. Corals play a crucial role by offering various habitats for the Lysmatidae, acting as refuges from predators and competitors (Idjadi & Edmunds 2006) and altering local hydrodynamics, thereby enhancing nutrient and zooplankton availability (Atkinson & Bilger 1992). This combination of factors may explain the equivalence in the number of species found in the Tropical Atlantic and Central Indo-Pacific realms. The presence of scleractinian corals in the Gulf of Mexico, Caribbean, and the Philippines (Roberts et al. 2006, Soetaert et al. 2016) coincides with the provinces with the highest richness of Lysmatidae. Recognized as ecosystem engineers, scleractinian corals can shape bottom topographies, with heights ranging from tens to hundreds of meters (Roberts et al. 2006, Soetaert et al. 2016).

Scleractinian corals reefs induce the upwelling of surface waters through the formation of internal waves or hydraulic jumps and construct extensive areas serving as habitats for sponges and fish (Soetaert et al. 2016). All of these ecosystem functions provided by corals are relevant for the Lysmatidae species that perform fish cleaning or exhibit symbiosis with anemones, such as *Lysmata amboinensis*, *L. grabhami*, *L. debelius*, *L. splendida*, *L. pedersenii*, *L. seticaudata*, *L. californica*, and *L. wurdemanni* (Calado et al. 2003, 2008, Rhyne & Lin 2006, Baeza 2013).

The relationship between bathymetry and Lysmatidae richness remained consistent across all scales, being more pronounced at finer scales (ecoregion and local) and may be associated with the coloration and behavioral aspects of the Lysmatidae. Coloration in crustaceans is regulated by cells containing chromatophores (Rao et al. 1985) and is influenced by both physiological and environmental factors (Kronstadt et al. 2013, Vega-Villasante et al. 2015). It serves various functions such as communication, camouflage, and thermoregulation (Kronstadt et al. 2013). Depth, as an example, can affect light penetration, and shrimp with reddish coloration can camouflage themselves better, increasing their crypticity (Kronstadt et

al. 2013). The reddish coloration pattern, as observed for the Lysmatidae in general, functions as camouflage for dark environments; when inhabiting shallow environments, the species tend to adopt nocturnal habits and remain hidden in crevices and caves (Calvo et al. 2016).

In the case of aposematic species, we expect the opposite pattern. Specifically, concerning the cleaner shrimps, we observe distinct coloration patterns associated with fish-cleaning behavior and reef habitat, typically shallow (Calado et al. 2003, Calado 2006). Evidence from *L. grabhami* and *L. amboinensis* suggests that part of the cues provided by shrimp to their 'clients' are visual and may be associated with visual patterns as a specific signal (Fletcher et al. 1995, Rufino & Jones 2001).

At the province and ecoregion scales, the best models incorporated all proposed hypotheses but diverged in the significance of each variable. At the province scale, both bathymetry and coral richness emerged as significant variables, mirroring their importance at the realm scale. On the other hand, salinity variation and anthropogenic impacts exhibited a negative relationship with Lysmatidae richness. The impact of salinity on the distribution the Lysmatidae richness has been substantiated, given the well-documented and regularly reviewed saline tolerance ranges of numerous decapods, including comprehensive studies by Lockwood (1962), Mantel & Farmer (1983), Charmantier et al. (2008), and Freire et al. (2008). It is established that fully marine groups, such as the Lysmatidae, function as osmotic conformers. In essence, the osmolarity of their hemolymph closely mirrors the ambient environment within a narrow range of variation (McNamara & Faria 2012). Consequently, Lysmatidae shrimps display limited regulatory capacity for both hemolymph concentration and composition, as well as osmotic urine production (McNamara & Faria 2012).

Considering that variations in water salinity and resource availability can function as stressors during the larval stages of marine shrimp (Giménez & Anger 2001), it is plausible that the stress effects from the environment could be passed down through generations, causing harm to juvenile stages, as outlined by Giménez (2006) in terms of 'phenotypic linkage' processes. This may hinder the establishment of certain species in regions with significant salinity variations or their ability to migrate through areas with such characteristics.

The discovery of contrasting anthropogenic impacts on Lysmatidae richness at different scales (province: negative, ecoregion: positive) under-

scores the significance of scale in biodiversity research. At most regional scales, a negative relationship between anthropogenic impact and Lysmatidae richness may be related to benthic marine ecosystems experiencing erosion in their ecological resilience due to climate change (Wernberg et al. 2010, Graham et al. 2015). Changes in physiological, demographic, and community processes due to temperature increase have led to species redistribution (Wernberg et al. 2010, Poloczanska et al. 2013).

At the finest scales, anthropogenically impacted marine environments could be characterized by an excessive influx of organic matter (wastewater, benthic cover mortality on hard substrates, fishing and tourism residues), promoting the proliferation of algae and pests. This increase in organic matter could also lead to an increase in the population of scavengers and natural cleaners, such as the Lysmatidae cleaning species (Calado & Narciso 2005).

At the ecoregion scale, we observed a positive effect of temperature range on the richness of Lysmatidae. This finding may be related to physiological aspects of the clade, as temperature plays a crucial role in establishing reproductive periodicity and recruitment in shrimps and numerous other crustaceans (Sastry et al. 1983, Bauer 1992). Seasonal recruitment is a common feature among crustacean species inhabiting temperate latitudes, a trait also observed in *Exhippolysmata oplophoroides* (Baeza 2010). This species displays a mixed pattern of reproductive biology, with embryo incubation occurring throughout the year and juvenile recruitment limited to the summer months (Baeza 2010).

Despite the negative relationship found between salinity range and richness at the province scale, this pattern does not hold at the ecoregion scale. This fact becomes evident when we observe the ecoregions of the northern Gulf of Mexico and tropical southwestern Atlantic, which maintain high Lysmatidae richness values despite receiving a substantial volume of fresh water from the Mississippi and the Amazon Rivers, respectively. It is conceivable that salinity variation northeast of the Gulf of Mexico influenced the isolation and speciation of the *L. wurdemanni* complex, as this river separates populations along the Florida coast from those along the Texas coast and may explain the observed speciation occurring between these populations. According to Baeza & Prakash (2019), the genetic distance between Texas and Florida populations was relatively large (p -distance = 0.045–0.081, mean \pm SD = 0.0645 ± 0.0011) and comparable to that calculated for species pairs within the genus *Lysmata*.

Although we did not find a relationship between mean temperature and Lysmatidae richness, we cannot dismiss the indirect effect of this variable, as coral richness is an important predictor for the clade, and mean temperature is directly related to it. Considering the decline in ecological resilience of benthic marine ecosystems promoted by climate changes, temperature emerges as a significant stressor across ecosystems (Wernberg et al. 2010, Graham et al. 2015). The reduction in extreme cold events in winter has facilitated the expansion of cold-sensitive tropical species into temperate regions (Cavanaugh et al. 2019). In the biogeographic division between tropical and temperate communities, global warming has led to the spread of tropical corals, fish, and benthic crustaceans (Poloczanska et al. 2013, Agostini et al. 2021).

Poloczanska et al. (2013) identified a benthic crustacean expansion rate of approximately 20 km per decade towards colder environments and emphasized that the reorganization of species at a regional scale can trigger cascade effects. González-Ortegón et al. (2020) suggested that the expansion of *L. unicolornis* to the western Atlantic coasts of Europe may be linked to the tropicalization of subtropical areas and warned against the spread of non-native species (Dawson et al. 2017), which could alter or create biological interactions, often leading to changes in the recipient community.

In conclusion, our study showed the significance of spatial scale in shaping richness patterns and revealed a bimodal distribution pattern for Lysmatidae, with peaks in tropical–subtropical transition regions and notably in the Gulf of Mexico and the Caribbean. We confirmed the effect of physiological stress (PSH) on the richness of Lysmatidae at regional scales (ecoregion and province) since salinity and temperature were negatively related to family richness. Contrary to our predictions, at the local scale, we noted the influence of bathymetry in promoting Lysmatidae richness, a pattern that persisted across other scales. The confirmation of anthropogenic impact also revealed varying influences across regional scales (ecoregion and province).

Furthermore, our research confirms the importance of habitat heterogeneity for the clade at broader scales, as we observed a positive relationship between coral richness and the Lysmatidae richness at larger scales. This finding underscores the significance of coral reef environments for Lysmatidae conservation efforts. Additionally, we emphasize the importance of expanding sampling efforts for the group to ensure the inclusion of all species in future studies.

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