PRIMARY RESEARCH PAPER

Global patterns and predictors of primary freshwater crab richness across taxa and realms

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Abstract Freshwater ecosystems are among the most important in the world and provide essential functions and services to humans. In this study, we examine the roles of environmental and historical factors in explaining contemporary patterns of species richness. We investigated spatial patterns of species richness of freshwater crabs by compiling geographic distribution maps for 1271 species. We employed six environmental variables slightly correlated and non-collinear to test environmental hypotheses. At a global scale, we identified three regions characterized by particularly high species richness: in northern South America (Neotropical biogeographic realm), in the Western Ghats and Sri Lanka (Oriental), and southwestern China (Oriental). The best-fitting model that explained global richness variation included environmental hypotheses: *Temperature-Speciation*,

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Resource Availability, *Habitat Heterogeneity* and *Anthropic Impact*. We also observed a historical influence on the pattern of richness, with distinct sets of environmental predictors of richness across taxa and biogeographic realms. Our models suggest that freshwater crab richness is associated with by varying processes occurring within specific environmental and historical scenarios. In general, we documented a concentration of freshwater crab richness in areas heavily impacted by human activities. These findings hold implications for the conservation of this taxonomic group.

Keywords Brachyura · Conservation · Diversity hotspots · Evolutionary history · Freshwater · Human impact

Introduction

For centuries, ecologists and biogeographers have described the patterns of richness in taxonomic groups at a global scale. However, a more considerable challenge is to understand the drivers of observed diversity patterns (Peters et al., 2016; Schluter & Pennell, 2017). The main ecological explanations for richness patterns at broad scales focus on the effects of environmental variables [e.g., temperature, precipitation, and productivity (Diniz-Filho et al., 2004; Jetz et al., 2004; Brehm et al., 2007; Belmaker & Jetz, 2015)], complexity of habitat [e.g., elevation, slope and roughness (Jetz et al., 2004; Romdal & Grytnes, 2007; Peters et al., 2016; Amatulli et al., 2018)], historical processes [e.g., climatic fluctuations, orogenic processes that influenced dispersal (Hawkins & Porter, 2003; Wiens & Donoghue, 2004; Buckley & Jetz, 2007; Morinière et al., 2016; Martinez et al., 2020)], and anthropogenic impacts [e.g., pollution, land use change, and overexploitation (Cardinale et al., 2012; Newbold et al., 2015; Dudgeon, 2019)].

Among the most discussed factors affecting the spatial variation of species richness, environmental temperature is the one receiving the most attention (Pontarp et al., 2019). There is broad support that temperature has a strong positive effect on richness, related to increased rates of biotic processes and evolutionary diversification of species (Rohde, 1992; Allen et al., 2002; Brown, 2014) (*Temperature-Speciation Hypothesis*). Alternatively, the integration of variables related to the availability of resources, such as water and food, has been frequent in the testing of hypotheses related to the variation of richness (Hawkins et al., 2003a). Precipitation is one of these variables related to water, which shows fundamental importance concerning the availability of water for the maintenance of biodiversity, especially in the tropics (see Wright, 1983; Hawkins et al., 2003a) (*Resource Availability Hypothesis*). Similarly, energy flow in food webs has a positive effect on population persistence and species coexistence (Mittelbach et al., 2001; Hurlbert & Stegen, 2014) (*Resource Availability Hypothesis*). In addition, several studies have also proposed that habitat heterogeneity is a determinant of the number of species due to elevated speciation rates at high heterogeneous habitats (Kerr et al., 2001; Rahbek & Graves, 2001; Jetz & Rahbek, 2002; García-Rodríguez et al., 2021). Consistent with this proposal, the high rate at which habitats change along an elevational gradient affects habitat diversity in regions with greater topographic variability, leading to increased regional species richness (Kerr & Packer, 1997) (*Habitat Heterogeneity Hypothesis*). Additionally, the *Historical Hypothesis* proposes that ecology and climate must act on evolutionary and biogeographical processes (e.g., speciation, dispersal, and extinction) to determine patterns of species richness (Wiens & Donoghue, 2004; Mittelbach et al., 2007; Wiens et al., 2009). Lastly, studies have shown in recent decades that habitat loss as a result of the destruction of natural systems by human actions is an undisputed main driver in the loss of biodiversity (Vitousek et al., 1997; Newbold et al., 2015) (*Anthropic Impact Hypothesis*). In this scenario of increasing impact on ecosystems and biodiversity, freshwater ecosystems are especially susceptible to environmental changes arising from multiple human activities (Dudgeon, 2019; Albert et al., 2020).

Freshwater habitats provide habitat for around 10% of all animal species (Balian et al., 2008). Understanding the diversity and distribution of freshwater organisms is critical for the conservation and management of biodiversity (Strayer & Dudgeon, 2010). Even though knowledge about freshwater biodiversity is improving (Collen et al., 2014; Turak et al., 2017; Faghihinia et al., 2021), most studies consider the diversity of individual taxa along different environmental axes, while comparative studies between taxa along the same patterns are scarce (e.g., Peters

et al., 2016). Furthermore, most of these studies have emphasized the global diversity patterns of vertebrate taxa, while for invertebrate taxa, many gaps remain unexplained, especially in tropical latitudes where an invaluable number of species await description (Dudgeon et al., 2006; Balian et al., 2008; Willig & Presley, 2018). However, some freshwater species have a wide geographic distribution, and the insular nature of freshwater habitats has led to the evolution of several species in restricted geographic areas (Strayer, 2006; Strayer & Dudgeon, 2010). Those areas often encompass only a single lake, river, or drainage basin, which may increase the risk of species extinction (Strayer, 2006; Strayer & Dudgeon, 2010). Thus, decapod crustaceans exhibit high levels of species richness and local endemism (Balian et al., 2008; Leprieur et al., 2011), resulting in a turnover of species between basins or watersheds, especially in tropical latitudes that were not affected by glaciation during the last ice age (Leprieur et al., 2011). For this reason, water bodies tend not to be replaceable regarding their fauna due to high species turnover, contributing to regional species richness (Dudgeon, 2012).

Freshwater crabs belong to seven families, six of which share hypothesized common ancestry: the Epiloboceridae, Deckeniidae, Gecarcinucidae, Potamonautidae, Potamidae, and Pseudothelphusidae. The seventh family, the Trichodactylidae, is positioned on a separate part of the Brachyuran phylogenetic tree (Cumberlidge & Ng, 2009; Tsang et al., 2014; Cumberlidge, 2016; Cumberlidge & Daniels, 2022). Members of all families, recognized as primary freshwater crabs, adopted freshwater, semi-terrestrial, or terrestrial lifestyles and can complete their life cycle independently of the marine environment (Yeo et al., 2008; Cumberlidge & Ng, 2009). Most of them are an indispensable component of the biodiversity found in freshwater ecosystems globally. At the same time, they are among the taxa most affected by global threats to biodiversity (Cumberlidge et al., 2009).

In this study, we evaluated different models composed of multiple environmental predictors to test which environmental hypothesis (i.e., *Temperature-Speciation Hypothesis*, *Resource Availability Hypothesis*, *Habitat Heterogeneity Hypothesis*, and *Anthropic Impact Hypothesis*), or which combination of these hypotheses, best elucidates the global pattern of primary freshwater crab richness. Additionally,

we analyzed whether there is an evolutionary signature in the global pattern of primary freshwater crabs (*Historical Hypothesis*). We expected to find distinct sets of environmental variables predicting the richness across taxa and biogeographic realms if there is an evolutionary and/or historical effect (Rangel et al., 2007; Belmaker & Jetz, 2015).

Material and methods

We obtained geographic distribution maps for 1287 extant species of freshwater crabs (Decapoda: Brachyura) from the IUCN Red List (www.iucnredlist.org). We revised in 19 April 2021 all species names using the World Register of Marine Species (WoRMS, available at http://www.marinespecies.org) and synonyms reconciled. We assigned the entire taxonomic information using the Taxize library (Chamberlain & Szöcs, 2013) in a final dataset consisting of 1271 species (~85% of extant species, Supporting Information A) (Tsang et al., 2014). These crabs are distributed across the six biogeographic realms: Afrotropical (Afr), Australian (Aus), Nearctic (Nea), Neotropical (Neo), Oriental (Ori), and Palearctic (Pal), which are commonly used in studies with freshwater organisms, (e.g., Lévêque et al., 2007; Crandall & Buhay, 2008; Yeo et al., 2008; Toussaint et al., 2016; Villéger et al., 2011).

For the present study analysis, we grouped the species of the families Deckeniidae and Epiloboceridae as representatives of Potamonautidae and Pseudothelphusidae, respectively. We performed such grouping due to the small number of species and, consequently, a small number of maps available in IUCN (Deckeniidae, 26 maps; Epiloboceridae, 5 maps; Supporting Information A). Also, such grouping was performed considering the great phylogenetic affinity between the families that were grouped (Álvarez et al., 2020; Cumberlidge & Daniels, 2022). Thus, Potamonautidae includes species from the family Deckeniidae, and Pseudothelphusidae includes species from Epiloboceridae. Importantly, it is known that recent studies have been proposing new hypotheses of relationships between these crabs (Álvarez et al., 2020; Wolfe et al., 2023) and that some species used in the present study may have their taxonomy revised (e.g., synonymized with others). In addition, other species may be

described based on studies in progress. However, for the main purpose of the present study, i.e., to evaluate hypotheses about predictors of macroscale richness, such taxonomic activity should have little or no implication on the results obtained here.

We overlaid the range maps onto a grid with cells having 1° resolution (~100×100 km at the equator) and estimated the species richness from the sum of overlapping distributional ranges in each grid cell. Maps were processed using the package 'raster' (Hijmans et al., 2021) in the R platform version 4.1.1. A buffer (with a threshold set at 75th percentile of the maximum richness per cell of each map) was applied to delineate the regions characterized by high richness of freshwater crabs (in global scales and across taxa and biogeographic realms).

We downloaded 13 candidate variables to compose our environmental hypotheses (Supporting Information B, Table B.1): eleven freshwater-specific environmental layers (elevation range, average elevation, slope range, average slope, number of upstream-stream grid cells, number of upstream-catchment grid cells, annual mean upstream temperature, mean upstream diurnal range, upstream isothermality, annual upstream precipitation, and upstream precipitation seasonality) from EarthEnv project (available at http://www.earthenv.org); Normalized Difference Vegetation Index (NDVI) from Earth Observatory (available at http://earthobservatory.nasa.gov/); and Human Footprint Index (HFI) from Socioeconomic Data and Applications Center (SEDAC; available at https://sedac.ciesin.columbia.edu/). However, these variables typically have strong collinearity, which may cause misinterpretations of environmental models involving multiple predictors (Terribile et al., 2009). Correlation between all possible combinations of the 13 downloaded layers was assessed by a Pearson's correlation analysis, and multicollinearity was assessed by calculating the variance inflation factor (VIF) using the 'usdm' package in R. When two or more variables were highly correlated, environmental layers with less biological interpretation, according to our hypotheses, were excluded (Supporting Information B, Table B.1 and B.2). We used a final set of six environmental layers slightly correlated (i.e., Pearson's $r < |0.5|$) and non-collinear (VIF < 5; Vicente et al., 2013) to test the following environmental and historical hypotheses (see the conceptual framework that support the environmental hypotheses in Fig. 1):

Temperature-Speciation Hypothesis (TSH) (Fig. 1)

[1] Annual mean upstream temperature (Hydro_1). Freshwater crabs are few or not found in ecosystems with colder water temperatures (Cumberlidge et al., 2011, 2014). According to Rohde (1992), the effect of temperature on physiological processes leads to faster rates of evolution and more rapid responses to selection in the tropics.

Resource Availability Hypothesis (RAH) (Fig. 1)

[2] Normalized Difference Vegetation Index (NDVI), [3] annual upstream precipitation (Hydro_12), and [4] upstream precipitation seasonality (Hydro_15). According to Cumberlidge et al. (2011, 2014), water availability (as a primary habitat resource) and vegetation cover (as a food supply resource) are important predictors of freshwater crab richness. RAH predicts that high primary productivity and water availability favor the coexistence of more species (Hawkins et al., 2003a, 2003b).

Habitat Heterogeneity Hypothesis (HHH) (Fig. 1)

[5] Elevation range (Dem_range) serves as a measure of habitat heterogeneity. Elevation exhibits multiple dependencies related to topographic complexity, micro/macroclimates, or land cover (Amatulli et al., 2018). Typically, mountainous regions feature a wide elevation range, marked by complex relief, diverse landscapes, mosaic of habitats, variable climatic conditions variable, and environmental diversity (Kozak & Wiens, 2006; García-Rodríguez et al., 2021; Hu et al., 2021; Li et al., 2022). HHH predicts that such conditions are likely to increase niche partitioning and would be associated with higher speciation rates and, consequently, higher levels of species richness (Komyakova et al., 2013; Gouveia et al., 2014; Perrigo et al., 2020).

Anthropic Impact Hypothesis (AIH) (Fig. 1)

[6] Human Footprint Index (HFI) which considers four types of data to measure human influence: population density, land transformation, human access, and power infrastructure. The human footprint is a quantitative measurement of humanity's impact on the Earth's land surfaces (Sanderson et al., 2002).

Fig. 1 Conceptual framework supporting our environmental hypotheses about changes in freshwater crab richness. Models are: TSH, *Temperature-Speciation Hypothesis*; RAH, *Resource Availability Hypothesis*; HHH, *Habitat Heterogeneity Hypothesis*; AIH, *Anthropic Impact Hypothesis*. NDVI, Normalized Difference Vegetation Index
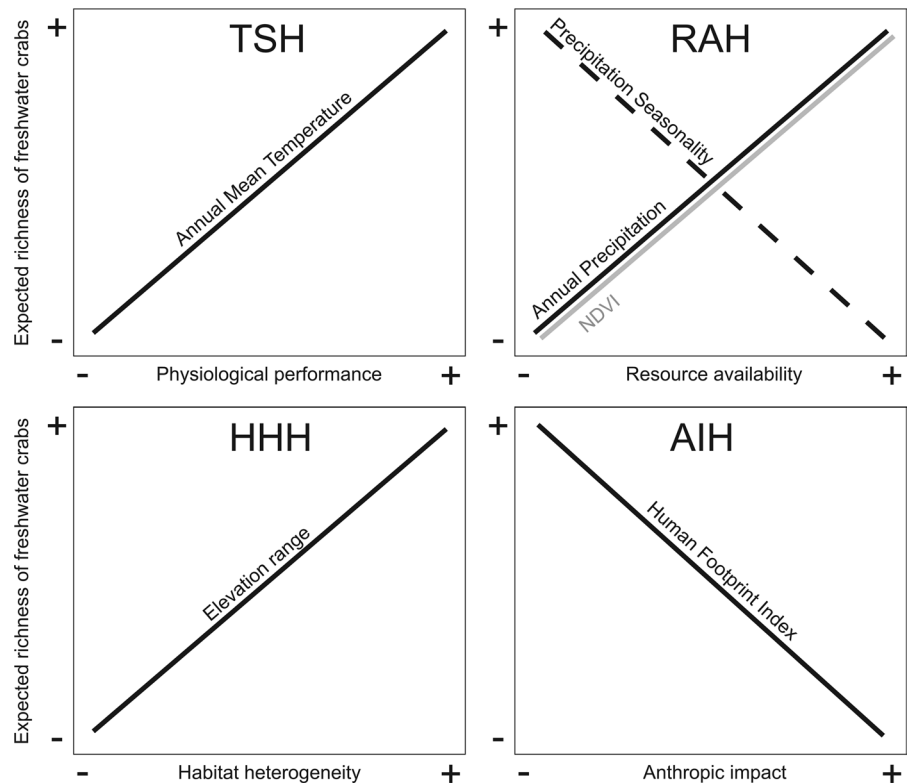
AIH is tested here considering the prediction that human influence is one of the most important factors negatively affecting life in the world (see Jacobson et al., 2019).

Historical Hypothesis (HIH)

We partitioned the global dataset, which comprises 1,271 species, into sub-datasets, according to: [1] taxon (i.e., Gecarcinucidae, Potamidae, Potamonautidae, Pseudothelphusidae, and Trichodactylidae), as a proxy for evolutionary history. Lineages tend to preserve their niches and associated ecological traits over evolutionary time (see phylogenetic niche conservation, Peterson, 1999; Wiens & Graham, 2005; Losos, 2008); [2] biogeographical realm (i.e., Afrotropical, Australian, Nearctic, Neotropical, Oriental, and Palearctic), as a proxy for the historical contingencies influencing geographical patterns of species richness, arising from differential rates of speciation and extinction in regional faunas (Hawkins et al., 2003b; Buckley & Jetz, 2007). Thus, if there is a historical effect on the richness pattern of freshwater crabs, we would expect the richness pattern of each taxon and

realm to be explained by idiosyncratic models rather than congruent models with that of other taxa and realms.

To test the environmental hypothesis or set of hypotheses, that best explain the variation in freshwater crab richness, models were constructed. So, we separately tested each environmental hypothesis (TSH, RAH, HHH, and AIH), as well as each possible combination among them (i.e., TSH + RAH, TSH + HHH, TSH + AIH, RAH + HHH, RAH + AIH, HHH + AIH, TSH + RAH + HHH, TSH + RAH + AIH, TSH + HHH + AIH, RAH + HHH + AIH, and TSH + RAH + HHH + AIH). The models were tested using Generalized Linear Models (GLMs) with multiple predictors. We corrected the potential effects of spatial autocorrelation in the response variable by using eigenvectors for spatial filtering (ESF) as covariables in our models. ESF is an effective method that can be adapted to GLMs to minimize spatial autocorrelation between different spatial scales (Diniz-Filho & Bini, 2005; Chun et al., 2016). In this method, we extracted n eigenvectors, which represent the spatial structure of our
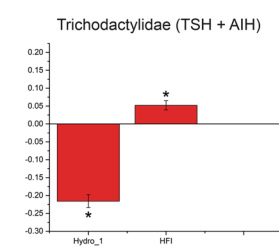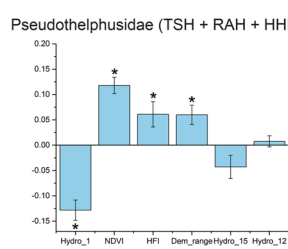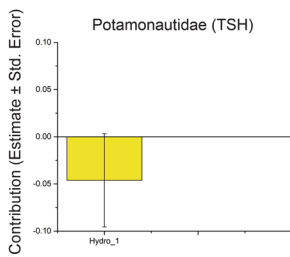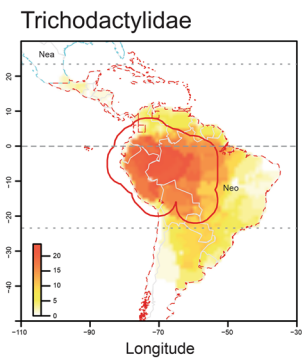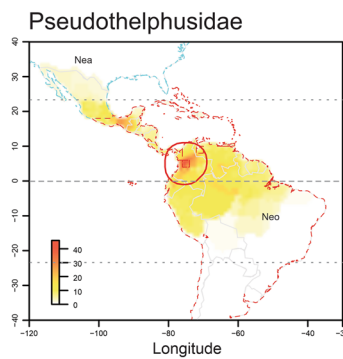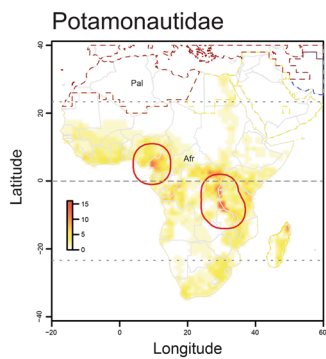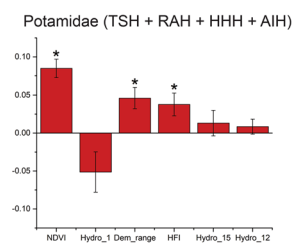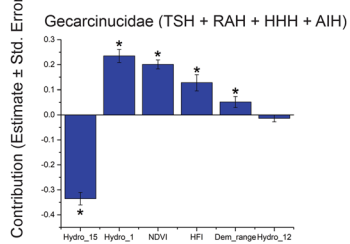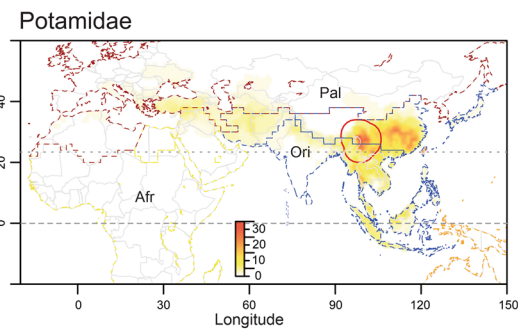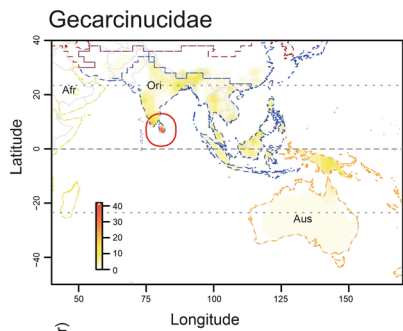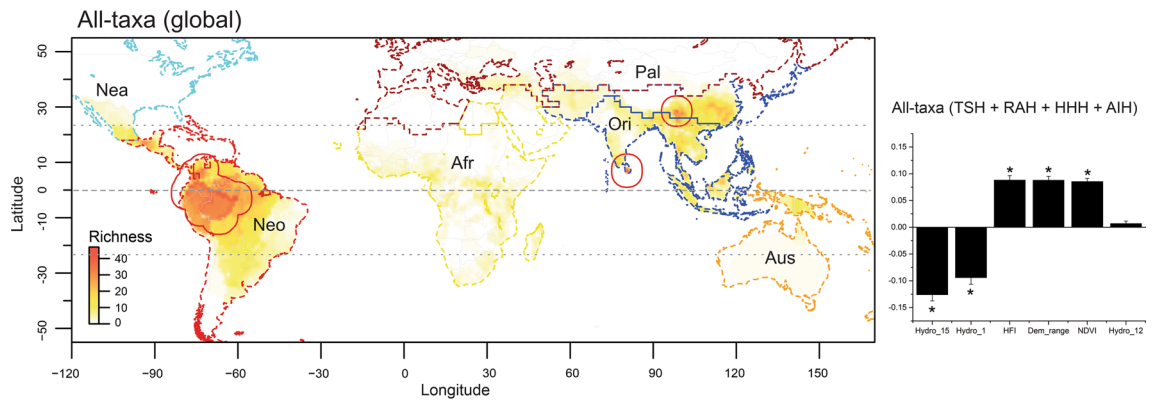
◄**Fig. 2** Patterns of freshwater crab richness at a global scale (all-taxa) and across taxa (Gecarcinucidae, Potamidae, Potamonautidae, Pseudothelphusidae, and Trichodactylidae). Red lines delimit main richness hotspots based on a buffer with a cut-off threshold at the 75th percentile of the maximum richness for each map cell. Afr, Afrotropical (yellow dashed line); Aus, Australian (orange dashed line); Nea, Nearctic (cyan dashed line); Neo, Neotropical (red dashed line); Ori, Oriental (blue dashed line); Pal, Palearctic (brown dashed line). The best-fitting model was selected using AIC corrected for the presence of spatial autocorrelation in the model residuals. * Indicates a significant relationship ($P<0.05$). Predictor variable codes are: Hydro_1, annual mean temperature; Hydro_12, annual precipitation; Hydro_15, precipitation seasonality; NDVI, Normalized Difference Vegetation Index; Dem_range, average elevation; HFI, Human Footprint Index. Legends: TSH, *Temperature-Speciation Hypothesis*; RAH, *Resource Availability Hypothesis*; HHH, *Habitat Heterogeneity Hypothesis*; AIH, *Anthropic Impact Hypothesis*

data. The set of eigenvectors was selected to maximize the determination coefficients (R^2) to avoid an overcorrection for spatial autocorrelation (Diniz-Filho & Bini, 2005; Chun et al., 2016). ESF analyses were conducted using the R package 'spdep'. The influence of spatial autocorrelation in model residuals was assessed by Moran's I coefficients (Diniz-Filho et al., 2004; Diniz-Filho & Bini, 2005). The Akaike's Information Criterion (AIC) was used to rank competing models and weigh the relative support for each one (Burnham et al., 2011). We calculated the delta AIC (ΔAIC) for each model as the different between the AIC of the candidate model (AIC_i) and the AIC with the minimum value ($_{min}AIC$). Then, we performed a model selection comparing AIC values to find model that best fit our data (ΔAIC=0). After ranking the models using the AIC criterion, the performance of the best models was assessed by examining the goodness-of-fit of models (R^2 values; see Table B.3 in Supporting Information B), taking into account the finite nature of data and, consequently, recognizing that models serve as approximations to reality (Burnham & Anderson, 2004). First, the above approach was used to explain species richness at global scale, considering all primary freshwater crabs. Second, to assess the *Historical Hypothesis*, we tested the best model that explains the patterns of freshwater crab richness across taxa and realms, considering each sub-dataset separately.

Results

Patterns of the richness

At the global scale, we identified three main biogeographic realms that harbor high concentrations of freshwater crab diversity, characterized by the presence of 35 or more freshwater crab species per map cell (see Fig. 2): [1] Neotropical: comprising a vast geographic area, situated in northern South America (northern Brazil, Venezuela, Colombia, Ecuador, and Peru); and two regions in the Oriental realm, with smaller area sizes, but which also concentrate great diversity; [2] Western Ghats and Sri Lanka; and [3] Yunnan region in southwestern China, which is the only area of great diversity outside the tropical zone, i.e., north of the Tropic of Cancer.

The regions where richness at the global scale coincide with those showing the highest richness in the following taxa: Gecarcinucidae (Western Ghats and Sri Lanka); Potamidae (in southwestern China); and Pseudothelphusidae and Trichodactylidae (northern South America) (Fig. 2). Additionally, these regions correspond to those with high richness in both the Oriental and Neotropical realms (Fig. 3). For details on the pattern of richness across taxa and realms, see Supporting Information B.

Predictors of the richness

The best model explaining the variation of freshwater crab richness at a global scale included the following hypothesis: *Temperature-Speciation, Resource Availability*, *Habitat Heterogeneity*, and *Anthropic Impact* (i.e., TSH+RAH+HHH+AIH) (Supporting Information B, Table B.3). We found that precipitation seasonality (Hydro_15) and annual mean temperature (Hydro_1) is negatively associated with species richness, while elevation, human impact, NDVI, and annual precipitation (Hydro_12) showed a positive relationship (Fig. 2, and Supporting Information B, Table B.4). When assessing individual hypotheses, *Resource Availability* was best supported by the data, with the precipitation seasonality (Hydro_15) is the most important predictor ($b=-0.181$; $P<0.001$).

Across taxa, we recorded a certain degree of congruence among the models that best explained the pattern of species richness. For three of the five taxa, the optimal model coincided with the one that
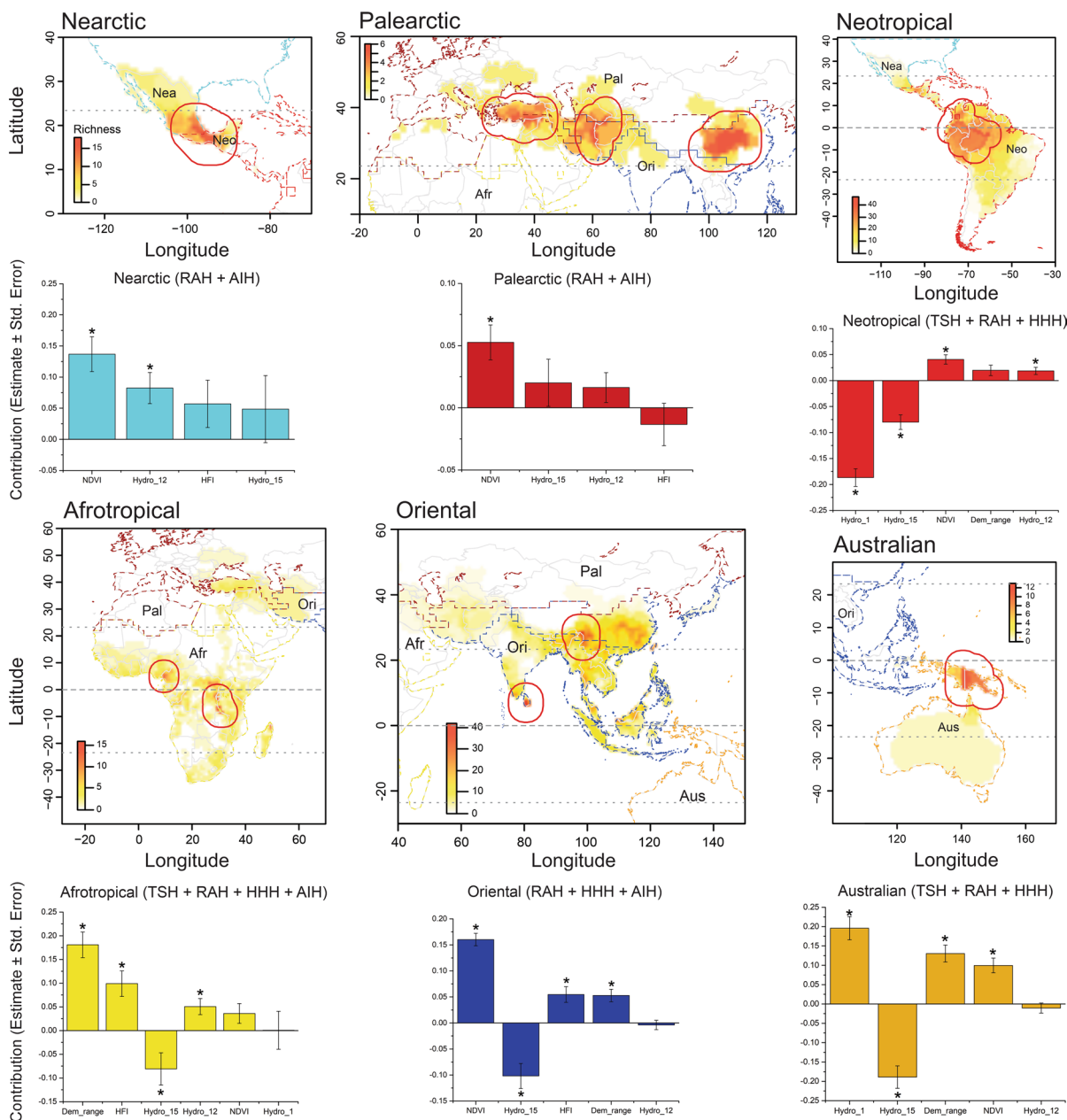
Fig. 3 Patterns of freshwater crab richness across biogeographic realms. Red lines delimit main richness hotspots based on a buffer with a cut-off threshold at the 75th percentile of the maximum richness for each map cell. Afr, Afrotropical (yellow dashed line); Aus, Australian (orange dashed line); Nea, Nearctic (cyan dashed line); Neo, Neotropical (red dashed line); Ori, Oriental (blue dashed line); Pal, Palearctic (brown dashed line). The best-fitting model was selected using AIC corrected for the presence of spatial autocorrela-tion in the model residuals. * Indicates a significant relationship ($P < 0.05$). Predictor variable codes are: Hydro_1, annual mean temperature; Hydro_12, annual precipitation; Hydro_15, precipitation seasonality; NDVI, Normalized Difference Vegetation Index; Dem_range, average elevation; HFI, Human Footprint Index. Legends: TSH, *Temperature-Speciation Hypothesis*; RAH, *Resource Availability Hypothesis*; HHH, *Habitat Heterogeneity Hypothesis*; AIH, *Anthropic Impact Hypothesis*

accounted for variations in richness at a global scale, i.e., TSH + RAH + HHH + AIH (see Fig. 2, and Supporting Information B, Table B.3). However, different variables were identified as having the most significant contribution to explaining the variation in richness across taxa (Fig. 2, and Supporting Information B, Table B.4). In each biogeographic realm, a distinct set of hypotheses and/or predictor variables was found to explain the variation in richness (see Fig. 3, and Supporting Information B, Table B.4). Nevertheless, for all realms, RAH constituted the model that provide the best explanation for the variation in richness, with precipitation seasonality (Hydro_15) and NDVI being among the most relevant variables in all biogeographic realms (Fig. 3, and Supporting Information B, Table B.4). For details on the predictors of richness across taxa and realms, see Supporting Information B.

Discussion

The distribution of primary freshwater crab species richness at a global scale (summarized in Fig. 2) is similar to the pattern observed in other freshwater taxa [e.g., fishes (Leprieur et al., 2011; Albert et al., 2020; He et al., 2020), and amphibians (Buckley & Jetz, 2007; Tisseuil et al., 2013)]. The species richness of freshwater crabs is concentrated in the tropical regions of the globe, as suggested by several previous studies (Yeo et al., 2008; Cumberlidge et al., 2009, 2011). Our analyses have identified three regions with particularly high species richness: [1] The Colombian and Ecuadorian Andes, and Amazon Basin (Neotropical realm); [2] Western Ghats and Sri Lanka (Oriental realm); [3] Yunnan in southwest China (Oriental realm). Such regions have been identified among those with the highest biodiversity of primary freshwater crabs in previous studies (Rodríguez & Magalhães, 2005; Cumberlidge et al., 2011, 2014; Shih & Ng, 2011; Magalhães et al., 2016).

On the other hand, the richness pattern of freshwater crabs observed in this study differs from those reported for crayfishes, which are concentrated in the Nearctic and Australian realms (Crandall & Buhay, 2008; Tisseuil et al., 2013). These differences appear to be associated with the effects of different mechanisms and evolutionary histories on the distribution of these distinct groups (Fetzner & Crandall, 2003;

Crandall & Buhay, 2008; Tsang et al., 2014; Owen et al., 2015). Most importantly, the present study is the first to evaluate the correlates of primary freshwater crab richness patterns, as discussed below.

The Neotropical realm

In the vast geographic region within the Neotropical realm that concentrates the richness of freshwater crabs, some of the ecosystems with high levels of biodiversity can be found, such as the Páramo and Amazon rainforest (Myers et al., 2000; Madriñán et al., 2013; García et al., 2019). Orogenic processes and sea-level changes produced intermittent land connections among islands and continental areas around the Caribbean Basin since the late Cretaceous. These events may have generated numerous opportunities for allopatric speciation, particularly in Pseudothelphusidae (see Álvarez et al., 2020). Our results indicate that Pseudothelphusidae exhibit great diversity in mountainous regions of Colombia and Ecuador, while Trichodactylidae exhibit great richness in the Amazon basin regions (see Fig. 2). These findings support patterns previously suggested by a previous study (see Rodríguez & Magalhães, 2005; Cumberlidge et al., 2014; Magalhães et al., 2016). These regions are characterized by forested mountains, topographic relief, and complex drainage systems that form river basins. These characteristics also promote genetic isolation and allopatric speciation.

The Oriental realm

The Oriental realm encompasses a significant portion of Asia, including Western Ghats and Sri Lanka, and Yunnan. Western Ghats and Sri Lanka region is considered one of 25 world biodiversity hotspots (Myers et al., 2000). This region has a rich ecosystem diversity due to its topographic and climatic heterogeneity and such ecosystem hosts a very distinct fauna assemblage with high levels of the richness of several groups [e.g., snakes and lizards (Botejue & Wattavidanage, 2012); amphibians (Batuwita et al., 2019); birds (Wijesundara et al., 2017); Gecarcinucidae freshwater crabs (Bossuyt et al., 2004; Klaus et al., 2014; Rajesh et al., 2017; Pati & Pradhan, 2020)]. In insular environments, although the habitat filtering process tends to favor better-adapted species, dispersal limitations cause the best competitor not

to reach all suitable locations, delaying competitive exclusion and favoring coexistence (Tilman, 1994; Hurtt & Pacala, 1995), and consequently, higher level of richness. Moreover, Sri Lanka was intermittently connected to mainland India during the Pleistocene ice ages and only 10,000 years ago, the present disruption was established (Rohling et al., 1998; Vaz, 2000). Then, past historical sea-level fluctuations have influenced migration and isolation patterns in the region, including for gecarcinucid crabs (Bossuyt et al., 2004). Studies have suggested distinct dispersal events, some of which may have involved transoceanic dispersal events, with historical implications for the freshwater crabs in island regions (Shih & Ng, 2011; Daniels et al., 2015; Daniels & Klaus, 2018). These suggestions also imply that ancestral forms of freshwater crabs may have been more tolerant of higher salinities than current forms (Daniels et al., 2006; Esser & Cumberlidge, 2011).

The Yunnan region is situated in southwest China, near the border with Myanmar, where two globally biodiversity hotspots converge: Indo-Burma and South-Central China (Myers et al., 2000). This area is the only one of the three identified in this study outside the tropical region with abundant rainfall, an elevational drop of 6135 m, and diverse microclimates (Chaplin, 2005; Yang et al., 2019). Several macroecological studies have demonstrated the relevance of these environmental characteristics as predictors of species richness for different animal groups (Rahbek & Graves, 2001; Diniz-Filho et al., 2004; Buckley & Jetz, 2007; Peters et al., 2016; García-Rodríguez et al., 2021). The Yunnan region also was suggested as the likely "center of origin" for the potamids of China and even East Asia (Shih & Ng, 2011).

Predictors of species richness patterns

At a global scale, our results support all tested hypotheses, except the *Anthropic Impact Hypothesis* (AIH) (see Fig. 1 and Supporting Information B, Table B.4 and Figure B.2). Anthropogenic impact exhibited a positive relationship with freshwater crab richness, contradicting the predictions of AIH. This result indicates a correlation but not necessarily a cause-and-effect relationship between anthropogenic impact and richness. Instead, our results indicate a significant portion of freshwater crabs inhabiting area under a high level of human impacts (see Fig. 2 and

Supporting Information B, Figure B12). These human impacts can consequently escalate threat patterns, primarily mediated by high rates of habitat loss and degradation, pollution, and overexploitation, particularly affecting species inhabiting freshwater environments (Collen et al., 2014).

We observed strong relationship between temperature, resource availability, habitat heterogeneity, and human impact with the global richness of freshwater crabs. On this scale, all predictor variables in the TSH + RAH + HHH + AIH hypothesis were significant with a strong level of support, except for annual precipitation (Hydro_12) (see Supporting Information B, Table B.4 and Figure B.2). Despite the lack of a significant effect of annual precipitation at a global scale, a significant effect was observed in biogeographic realms known to have higher annual precipitation, such as the Neotropical and Afrotropical realms (see Dantas & Fonseca, 2023). Areas with high annual precipitation rates often develop rich forests (Liu et al., 2021), which can provide habitat (e.g., rivers, streams, and stagnant ponds), access to refuge (e.g., on the forest floor or, in some cases, even in trees), and food resources (e.g., plant matter) for freshwater crabs (Yeo et al., 2008). Furthermore, precipitation seasonality had a negative effect on the richness of freshwater crabs, which may support empirical evidence that specializations (e.g., reproductive and physiological adaptations) are necessary for crabs to occupy areas with high rainfall intermittency (Gherardi & Micheli, 1989; Okano et al., 2000; Rios et al., 2022).

We also found support for *Historical Hypothesis* (HIH), as the drivers of richness vary across taxa and realms (see Supporting Information B, Figure B.2 and B.3). Our analysis showed that each taxon and realms have specific richness pools, attributed to differential in situ diversification (Smith et al., 2005). The species richness patterns recorded revealed that there is no general model or set of predictors to explain diversity patterns across taxa and realms. Instead, patterns and predictors of freshwater crab richness are idiosyncratic rather than uniform across taxa and realms. This singular relationship between taxa and environmental factors may be a consequence of taxon-specific resource requirements and adaptations to the environment. Such singularities across taxa are explained by niche conservatism, that is, the tendency of lineages to retain their niches and related

ecological traits over evolutionary time (Wiens & Graham, 2005; Kozak & Wiens, 2010), leading to phylogenetic autocorrelation in environmental distributions (Kozak & Wiens, 2010; Wu et al., 2014). Furthermore, the distinct richness pattern observed across biogeographic realms can also be attributed to differences in speciation and extinction rates (i.e., distinct regional evolutionary histories) (see Buckley & Jetz, 2007). These historical factors likely contributed to the disparities in freshwater crab species richness across regions.

However, much of the variation in richness patterns remains to be elucidated (see Supporting Information B, Table B.3), particularly within the Potamonautidae family (including Deckeniidae) and in the Afrotropical realm. It is necessary to incorporate information from biotic interactions to develop more comprehensive causal models. Importantly, some freshwater crabs can engage in or may be subject to interspecific competition for habitats, including with representatives of other taxonomic groups, such as crayfish (Yeo et al., 2008; Shih & Ng, 2011; Zeng & Yeo, 2018, and references therein).

Freshwater crab richness in a changing world

Two results of the present study support suggestions from previous studies that the diversity of freshwater crabs is threatened not only in the current environmental scenario (Cumberlidge et al., 2011, 2014; Magalhães et al., 2016; Cumberlidge & Daniels, 2018), but also in future scenarios due to anthropic impacts in progress (Yeo et al., 2008; Cumberlidge et al., 2009; Zeng & Yeo, 2018). Firstly, within the current environmental scenario, there was a positive correlation between freshwater crab richness and the Human Footprint Index (HFI). This finding does not imply a cause-effect relationship but rather suggests that areas with high concentrations of freshwater crab richness are also significantly influenced by human activities. The HFI employed in this study encompasses eight human pressures: built environments, population density, night lights, agricultural land, pastures, and accessibility via roads, railways, and waterways (Williams et al., 2020). We propose that freshwater environments that concentrate the richness of freshwater crabs also support various human activities. Hence, areas where water resources are essential for the production of goods and services

for society may require increased efforts to conserve freshwater crab biodiversity. Second, in a future environmental scenario, the diversity of freshwater crabs is also threatened, considering that the predictors related to resource availability were those with the highest explanatory power for the variation in richness. In this context, changes in regional precipitation and hydroclimate are among the most relevant impacts of climate change (Marvel & Bonfils, 2013; Zappa et al., 2020). In terms of climate change effects on freshwater decapods, a recent review by Toh et al. (2022) identified a few other effects besides rainfall changes. It has already been noticed that changes in rainfall patterns are altering the geographic areas of many plants and animal species, the time of their life cycle, and potential interspecific interactions between native and invasive species (Marvel & Bonfils, 2013; Zeng & Yeo, 2018; Weiskopf et al., 2020). Moreover, the high rates of deforestation and habitat degradation should also be a real concern for conservation of freshwater crab diversity in future environmental scenarios, considering that plant material is among the main food resources for most of these crabs (Yang et al., 2020a, 2020b). As an alternative hypothesis, we propose that the positive correlation between freshwater crab richness and the HFI could potentially be an artefact of somewhat biased sampling effort, i.e., because the areas of high HFI are also much more accessible for collection/sampling of freshwater crabs, whether for scientific purposes or socio-economic (e.g., ornamental trade, live food or medicinal trade, etc.). Future studies should investigate and potentially elucidate the causality of the correlation between HFI and freshwater crab richness.

Some areas with exceptionally high levels of freshwater crab richness are situated within hydrographic basins that provide multiple essential ecosystems services to humans [Amazon basin (Cumberlidge et al., 2014; Magalhães et al., 2016); Yangtze basin (Yang et al., 2009; Cumberlidge et al., 2011; Shih & Ng, 2011); Congo basin (Daniels & Klaus, 2018)]. Impacts on the biodiversity of these ecosystems are expected to affect the economy, health, and well-being of millions of people around the world. Therefore, the high rates of deforestation and habitat degradation of these ecosystems, as well as changes in climate, must be accompanied by an increase in adequate governmental policy and proper conservation planning. Studies that project the distribution of

freshwater crabs under different climate change and land use scenarios should be conducted to better the prediction of the impact of these threats in the future.

Author contributions DFRA was involved in the conceptualization, methodology, writing—original draft, writing—review and editing, investigation, and resources; PAM contributed to the conceptualization, methodology, writing—review and editing, and visualization; CM, SPBA and ACA assisted in writing—review and editing and visualization; TF was involved in the conceptualization, methodology, writing—review and editing, and visualization.

Data availability Data used in the analyses are provided in Supplementary Material.

Declarations

Conflict of interest Authors have no conflicting or competing interests.

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