Delineating freshwater fish biogeographic regions in the Philippine archipelago

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The Philippines, a biodiversity hotspot with a complex geological history, presents an ideal setting to study freshwater fish biogeography in archipelagos. Despite its ecological significance, analyses of freshwater fish distribution patterns across the archipelago remain lacking. This study addresses this knowledge gap by delineating native freshwater fish biogeographic regions in the Philippines and investigating the factors influences these patterns. This research integrates extensive native freshwater fish occurrences data with environmental variables and historical biogeography. Species distributions, diversity and endemism were analyzed using cluster analysis of Simpson's beta (βsim) dissimilarity matrix and Generalized Dissimilarity Modeling (GDM). The analysis identifies five distinct biogeographic provinces across the archipelago: Northern Luzon, Central/Southern Luzon, Greater Visayas, Palawan-Mindoro, and Mindanao. Geographic distance and Pleistocene Aggregate Island Complex (PAIC) grouping emerged as key drivers of fish species turnover. Indicator species analysis characterized the unique faunal composition of each province. This study provides the first comprehensive biogeographic framework for Philippine freshwater fishes, offering crucial insights for understanding evolutionary processes, guiding conservation planning, and informing management strategies in this megadiverse yet understudied region. The findings contribute to understanding freshwater biogeography in complex island systems while highlighting the importance of integrating historical and contemporary factors in explaining biodiversity patterns.

Keywords: assemblage; islands; map; Southeast Asia; tropical

Introduction

Freshwater ecosystems cover less than 1% of the Earth’s surface but support disproportionately high percentage of global biodiversity (Strayer and Dudgeon, 2010). The Philippines, an archipelago of over 7,600 islands, is no exception to this pattern. With its complex geography, tropical climate, and unique geological history, the country boasts a rich array of freshwater habitats, from mountain streams to lowland rivers and lakes, each supporting distinct assemblages of aquatic life shaped by both contemporary ecological processes and historical biogeographic events.

The concept of biogeographic regions, areas characterized by distinctive evolutionary histories, species assemblages, and environmental features, has proven invaluable in understanding large-scale patterns of biodiversity distribution and evolution (Holt et al., 2013). In the context of freshwater systems, biogeographic regions can be particularly useful for elucidating the interplay between current ecological conditions and historical processes in shaping the distribution patterns of aquatic organisms, including fish (Abell et al., 2008; Stelbrink et al., 2012 Tedesco et al., 2017).

While extensive research on freshwater biogeography has been conducted in continental systems, the delineation of such regions in complex archipelagos like the Philippines remains largely unexplored. This knowledge gap is particularly striking given the Philippines' status as a biodiversity hotspot. The archipelago's location at the intersection of several biogeographic realms, coupled with its geological history of island formation, isolation, and connectivity, has led to high levels of endemism and unique distribution patterns among its fauna (Heaney, 1986; Vallejo, 2011; Brown et al., 2013).

The Philippines presents a unique challenge and opportunity for biogeographic analysis. Its fragmented landmass, varied topography, and diverse climatic conditions have created a mosaic of freshwater habitats. From the extensive river systems of Luzon and Mindanao, to the numerous crater lakes scattered across the archipelago, each water body potentially hosts distinct fish communities shaped by local environmental conditions, dispersal events, and long-term evolutionary processes. Moreover, the archipelago's geological history is marked by periods of connection and isolation due to sea level fluctuations during the Pleistocene period which resulted in the formation of larger aggregate islands, known as Pleistocene Aggregate Island Complexes (PAICs) (Heaney, 1985; Robles, 2013). These PAICs (Figure 1) which included Greater Luzon, Greater Palawan, Mindoro, Greater Negros-Panay, Greater Mindanao and Sulu Archipelago, add a layer of complexity to the biogeographic patterns of its freshwater fauna (Brown and Diesmos, 2002).

Despite the ecological and evolutionary importance of Philippine freshwater ecosystems, comprehensive studies on the distribution patterns and biogeographic classification of freshwater fishes across the archipelago are lacking. While there have been localized surveys and taxonomic studies (e.g., Herre, 1924; Conlu, 1986), a broader, integrative approach to understanding freshwater fish distributions at the national scale, incorporating both ecological and historical factors, remains to be undertaken. Thus, this study aims to address this knowledge gap by: 1) compiling and analyzing existing data on freshwater fish distributions across the Philippines, 2) identifying distinct freshwater fish biogeographic regions based on similarities in species composition, environmental factors, and historical connectivity, 3) investigating the relationships between fish distribution patterns and key environmental variables, and 4) examining the influence of historical biogeography, particularly PAICs, on current distribution patterns. Lastly, the implications of these biogeographic regions for understanding evolutionary processes, conservation planning, and management in the Philippines are discussed.

Materials and Methods

Study Area

The Philippines is an archipelago located in Southeast Asia and comprised of 7,641 islands (Baldia et. al., 2017; Romeroso et. al., 2021), with a total land area of approximately 300,000 km² (Figure 1) (Amoroso, 2012). The archipelago is characterized by complex topography, ranging from coastal lowlands to mountain ranges. The geological history of the Philippine archipelago is complex and diverse, playing a crucial role in shaping its current biodiversity patterns. The islands have a heterogeneous origin, with some formed through volcanic activity, others through tectonic uplift, and some with continental origins (Voris, 2000; Hall, 2002). The archipelago can be broadly divided into three geological components: The eastern portion, including parts of Luzon and eastern Mindanao, originated from volcanic island arcs formed during the Cretaceous to early Tertiary periods (Voris, 2000; Pubellier et al., 2004). The western portion, including Palawan and parts of Mindoro, is composed of continental fragments that rifted from the southeastern margin of continental Asia during the opening of the South China Sea in the Oligocene (Yumul et al., 2003). The central Philippines, including the Visayas, represent a complex amalgamation of island arc systems and ophiolite complexes (Aurelio et al., 2013).

The Philippines boasts a rich diversity of inland waters, encompassing a wide array of aquatic ecosystems. There are 421 principal river basins throughout the archipelago, of which 19 are considered major river basins with catchment areas greater than 1,400 km² (DENR, 2013; BMB DENR, 2016; Hamel, 2018). The largest and most significant of these is the Cagayan River System in Luzon, which boasts a drainage area of approximately 27,280 km². Other notable river systems include the Agusan and Rio Grande de Mindanao Rivers in Mindanao, and the Pampanga River in Luzon (Ong et al., 2002). The country also hosts numerous lentic systems, including natural lakes, man-made reservoirs, and wetlands. These standing water bodies vary greatly in size, depth, and origin. The country has several significant lakes, which include Laguna de Bay being the largest freshwater lake at 900 km^2, Lake Lanao in Mindanao, Lake Taal in Luzon (a crater lake), and Lake Mainit, the country's deepest lake (Papa and Briones, 2017).

Fish Data

A comprehensive dataset of freshwater fish species occurrences across the Philippines was compiled, spanning nearly a century of ichthyological research. The data collection encompassed historical surveys, including the seminal works by Herre (1924, 1953), which provided a foundational understanding of Philippine freshwater fish distributions and taxonomy. Recent taxonomic studies were incorporated, with the primary species list derived from Jamandre (2023). Occurrence data was extracted from global biodiversity databases such as the Global Biodiversity Information Facility (GBIF, 2023) and FishNet2 (2023). An extensive literature search was conducted, including a thorough review of peer-reviewed literature, regional ichthyological journals, ecological surveys, and conservation reports. For the list of literature included in the dataset, see the references listed in Jamandre (2023). Where possible, data from recent field surveys conducted by the research team and collaborators was incorporated, ensuring the inclusion of the most current distribution information.

The dataset included all native freshwater fishes, encompassing primary freshwater, diadromous, and euryhaline species that spend at least part of their life cycle in freshwater environments. Non-native and introduced species were excluded from the analysis, a decision based on the potential of non-native species to confound biogeographic patterns and their inability to reflect the natural evolutionary and dispersal processes that have shaped the distribution of native fauna (Leprieur et al., 2008; Vitule et al., 2009). Furthermore, introduced species often have different ecological requirements and dispersal capabilities compared to native species, which can lead to biased interpretations of biogeographic patterns (Olden et al., 2010). For analysis purposes, the presence/absence data of native species at the catchment level was used.

Catchment Boundaries and Environmental Data

Catchment boundaries or units were delineated using multiple sources. The primary catchment unit used in the analysis was level-7 HydroBASINS (Linke et al., 2019), supplemented by data from Boothroyd et al. (2023). Boundaries were further refined based on traditional river delineations (e.g., Cagayan River, Agno, and Pampanga Rivers) and the Philippine ecogeographic maps (BMB-DENR, 2016). Integration of smaller tributaries and poorly researched rivers considered fish distribution quality, geomorphological features, and coastal river size. QGIS ver. 3.34 (QGIS, 2023) was utilized for catchment unit delineation.

Three categories of environmental data were collected to explore potential drivers of freshwater fish distribution patterns. Geographic and topographic variables included geographic distance between catchments, catchment area, mean stream length, drainage density, mean catchment elevation and slope. Topographic data were obtained from Boothroyd et al. (2023). Climate data were sourced from the Philippine Atmospheric, Geophysical and Astronomical Services Administration (PAGASA, 2024), including variables such as annual mean and maximum temperature, annual precipitation, and precipitation seasonality. To test the PAIC hypothesis, the classification of Pleistocene Aggregate Island Complexes as defined by Brown and

Diesmos (2002) was used, allowing investigation of whether freshwater fish diversity patterns align with the archipelago's paleo-geographic history. Catchment units were categorized based on which PAIC group they belong to (Figure 1).

Cluster Analysis

A matrix of Simpson's beta (βsim) species turnover was generated for all pairwise catchment combinations. Simpson's beta was chosen to minimize the effect of unequal sampling effort across the study area (Tuomisto, 2010; Shelley et al., 2019), which is common in poorly studied regions like the Philippines. Using the βsim pairwise distance matrix, an agglomerative cluster analysis was performed to generate a WPGMA (weighted pair-group method using arithmetic averages) hierarchical dendrogram in the software Biodiverse ver. 4.3 (Laffan et al. 2010). This allowed visualization of relationships between catchments based on species composition similarity and determination of a bioregionalization scheme for the Philippines.

Species Richness and Corrected Weighted Endemism

Species richness (SR) and corrected weighted endemism (CWE) were calculated for each catchment also using Biodiverse ver. 4.3. SR represents the approximate number of species present in each catchment, providing a measure of local diversity. CWE was calculated in relation to the entire Philippine archipelago, allowing identification of areas of high endemism within the country. CWE considers both the number of endemic species and their range sizes, giving higher weight to species with restricted distributions. This metric helps identify areas that not only have a higher number of endemic species but also those that harbor species found nowhere else in the Philippines.

Generalized Dissimilarity Modelling

Generalized Dissimilarity Modeling (GDM) was employed to investigate the environmental drivers of freshwater fish distribution patterns across the Philippines. GDM is particularly suited for analyzing large-scale ecological data as it can handle non-linear relationships between environmental variables and compositional dissimilarity (beta diversity). This method uses I-splines to model these non-linear relationships, allowing for a flexible representation of how species turnover varies along environmental gradients (Ferrier et al., 2007; Mokany et al., 2022).

In this analysis, predictor variables were grouped into three categories and independently modeled: (1) geographic and topographic factors (e.g., current geographic distance, catchment features), (2) climatic variables, and (3) historical biogeography (catchment PAIC grouping). Prior to model fitting, collinearity between predictors was assessed using Spearman correlations, retaining variables with correlations below ±0.7. The analysis used Simpson's beta dissimilarity matrix to quantify compositional differences between sites.

GDM was implemented using the 'gdm' R package (Manion et al., 2018), utilizing default settings for I-splines, which typically employs three I-spline basis functions per predictor. Model performance was evaluated based on the percentage of deviance explained, and the significance of individual predictors was assessed using permutation tests. Variation partitioning was used to determine the relative importance of geographic, topographic, climatic, and historical factors.

Indicator Species Analysis

To identify species characteristic of each delineated ecoregion, an indicator species analysis was performed as proposed by Dufrêne and Legendre (1997) using the indicspecies package (De Caceres and Legendre, 2009) in R software. This method calculates an indicator value (IndVal) for each species within defined groups, in this case, the biogeographic provinces. This IndVal index is based on two components: specificity (the probability that a given catchment belongs to a particular biogeographic province, given the presence of the species) and fidelity (the probability of finding the species in catchments belonging to that biogeographic province). The IndVal is the product of these two components and ranges from 0 to 1, with higher values indicating stronger associations between a species and a biogeographic province. To assess the statistical significance of these associations, a permutation test with 999 iterations was employed. Associations between species and biogeographic provinces were considered significant at $p < 0.05$. This analysis allows the identification of species that are most representative of each biogeographic province, providing insights into the characteristic fauna of different regions within the Philippine archipelago.

Results

Delineation of Freshwater Fish Biogeographic Provinces

The agglomerative cluster analysis based on Simpson's beta (βsim) species turnover matrix revealed five distinct biogeographic provinces for freshwater fish in the Philippines (Table 1; Figure 2). The resulting WPGMA hierarchical dendrogram (Figure 2) identified the following provinces: Northern Luzon, Central/Southern Luzon, Greater Visayas, Mindanao, and Palawan-Mindoro.

Northern Luzon, comprising four catchments, has the highest branch length (0.602), suggesting the greatest dissimilarity from other clusters. Palawan-Mindoro, also with four catchments, showed the second-highest branch length (0.567). Mindanao, encompassing eight catchments, displayed an intermediate branch length of 0.54.

Central/Southern Luzon (9 catchments) and Greater Visayas (7 catchments) both exhibited branch length values of 0.502, indicating similar levels of distinctiveness within the cluster analysis.

Species Richness and Endemism

The analysis of species richness (SR) and corrected weighted endemism (CWE) revealed distinct patterns across the identified biogeographic provinces (Figure 3, Table 1). Northern Luzon province exhibited moderate diversity and endemism, with SR ranging from 32 to 55 species and CWE values between 0.127 and 0.230. Central/Southern Luzon demonstrated the widest range of species richness among all provinces, varying from 24 to 105 species across its nine catchments. However, its CWE values were relatively lower, ranging from 0.095 to 0.191, indicating that while the region hosts high diversity, it may have fewer highly range-restricted species. Greater Visayas showed intermediate levels of both SR and CWE, with species richness varying between 34 and 98 and CWE values from 0.120 to 0.181 across its seven catchments. Mindanao presented an intriguing pattern with moderate SR (25 to 75 species) but the widest range of CWE values (0.088-0.388) among all provinces, suggesting the presence of both areas of low endemism and potential endemism hotspots within its eight catchments. Notably, the Agus River/Lanao Lake catchment within the Mindanao biogeographic province stands out as a hotspot of endemism, with the highest recorded CWE score of 0.388. The Palawan-Mindoro province stood out with the highest lower bounds for both SR (55-72 species) and CWE (0.150-0.279), indicating consistently moderate to high levels of both overall diversity and endemism across its four catchments.

Generalized Dissimilarity Modelling

The Generalized Dissimilarity Modeling (GDM) revealed that a combination of geographical, climatic and historical biogeographical factors may explain the distribution patterns of freshwater fish diversity in the Philippines (Table 2). Geographic and topographic variables explained 38.5% of the deviance in fish distribution patterns. Among these, geographic distance emerged as the most important predictor (24.163% deviance explained, $p < 0.001$) (Figure 4), indicating a strong effect of spatial separation on community composition. Interestingly, mean elevation also showed a notable contribution, although it was not statistically significant. PAIC groupings appear to be an important crucial factor in fish distribution patterns as well. This predictor showed a high importance value and was highly significant ($p < 0.001$), indicating a strong influence of historical biogeography on current fish diversity patterns. On the other hand, climatic variables only accounted for 9.72% of the deviance explained. Maximum temperature was the most important climate predictor (10.555% deviance explained), though not statistically significant. Annual rainfall and mean temperature had smaller contributions and were not statistically significant.

Indicator Species Analysis

To characterize the unique faunal composition of each biogeographic province, we conducted an Indicator Value (IndVal) analysis. Out of the 309 fish species in our dataset, 55 showed significant associations with specific biogeographic provinces (Table 3). The analysis revealed distinct assemblages of indicator species for each of the five major biogeographic provinces.

The analysis identified 10 indicator species for Northern Luzon. The strongest indicators were two Anguillidae species: *Anguilla japonica* (IndVal = 0.943, $p = 0.001$) and *A. luzonensis* (IndVal = 0.904, $p = 0.001$). Other significant indicators included

Mugilidae species such as *Crenimugil crenilabis* (IndVal = 0.849, p = 0.001) and *Mugil cephalus* (IndVal = 0.707, p = 0.003). The presence of these species suggests a strong marine influence on the freshwater ecosystems of Northern Luzon, possibly due to the region's coastal geography and river systems that facilitate the movement of catadromous and euryhaline species.

Seven species were identified as indicators for the Central/Southern Luzon region. The catfish *Arius manillensis* and the silver perch *Leiopotherapon plumbeus* emerged as the strongest indicators (both with IndVal = 0.837, p = 0.001). Notably, this region harbors the endemic species *Mistichthys luzonensis* (IndVal = 0.632, p = 0.021), highlighting the unique evolutionary history of this area. The presence of *Gobiopterus brachypterus* and *Zenarchopterus philippinus* further underscores the importance of estuarine habitats in this region.

The Greater Visayas province was characterized by nine indicator species, representing a diverse array of marine, estuarine, and freshwater habitats. The snake eel *Ophichthus polyophthalmus* showed the strongest association with this region (IndVal = 0.894, p = 0.001), followed by the goby *Glossogobius bicirrhosus* (IndVal = 0.845, p = 0.001). The presence of both demersal marine species (e.g., *Cynoglossus puncticeps, Lutjanus malabaricus*) and freshwater-associated taxa (e.g., *G. aureus*) reflects the complex aquatic landscape of the Visayan islands.

Nine species were identified as indicators for Mindanao. The region showed a strong association with eels, with *A. bicolor* emerging as the most significant indicator (IndVal = 0.913, p = 0.001). Other eel species, *A. borneensis* and *A. celebesensis,* were also important indicators. The presence of the catfish *Clarias macrocephalus* (IndVal = 0.833, p = 0.002) and the cyprinid *Barbodes binotatus* (IndVal = 0.773, p = 0.001) suggests a well-developed freshwater fish fauna. The diversity of indicator species, including both primary freshwater fishes and species with marine affinities, reflects Mindanao's complex geological history and diverse aquatic habitats.

The Greater Palawan-Mindoro province exhibited the highest number of indicator species (19), suggesting a highly distinct ichthyofauna. Many species showed a consistent level of association with this region (IndVal = 0.577, $p < 0.05$), including several endemics such as *Barbodes palavanensis, Dermogenys palawanensis,* and *Stiphodon palawanensis*. The strongest indicators were *Gobiosoma pallida* and *Rasbora argyrotaenia* (both with IndVal = 0.816, $p = 0.001$). It should be noted, however, that *G. pallida* may warrant taxonomic evaluation. Nonetheless, its statistical association with the region supports its potential biogeographic relevance. The presence of multiple *Barbodes, Rasbora* and other primary freshwater fish species (e.g., *Nematabramis alestes*) indicates a strong Sundaic influence on the freshwater fish fauna of this region.

Discussion

Philippine Freshwater Fish Biogeographic Delineation

This study represents the first biogeographic analysis specifically focused on freshwater fishes in the Philippines, filling a significant gap in our understanding of aquatic biodiversity patterns in the archipelago. The delineation of five distinct biogeographic provinces for native freshwater fishes, each with differing assemblages and endemism patterns at various degrees, provides significant insights into the ecological dynamics of this megadiverse region.

The identification of five biogeographic provinces (Northern Luzon, Central/Southern Luzon, Greater Visayas, Mindanao, and Palawan-Mindoro) refines previous biogeographic hypotheses for the Philippines (Brown et al., 2013). This delineation reflects not only historical influences but also contemporary environmental and ecological factors that shape freshwater fish distributions.

Northern Luzon Province

The Northern Luzon province is characterized by its mountainous terrain, dominated by the Cordillera and Northern Sierra Madre ranges. These features create a diverse array of aquatic habitats, including high-gradient streams, waterfalls, and isolated headwater systems. The pronounced endemism in this region may be attributed to the isolating effects of these topographic barriers, which limit dispersal and promote speciation (Heaney et al., 2016). The unique geological history of Northern Luzon, as the first major island to emerge in the Philippine archipelago, has allowed for prolonged periods of isolation and in situ diversification (Hall, 2002).

The indicator species assemblage in Northern Luzon is characterized by a strong presence of catadromous and euryhaline species, particularly eels (*A. japonica* and *A. luzonensis*) and mullets (*C. crenilabis* and *M. cephalus*). This pattern suggests strong connectivity between freshwater and marine ecosystems in the region, highlighting the importance of maintaining unobstructed river-ocean connections for these species' life cycles. The diversity of indicator species, ranging from *Anguilla* to coastal-associated fishes, indicates a heterogeneous array of habitats from upper river reaches to estuaries, likely contributing to the region's biodiversity. The strong association with *A. japonica*, typically found in East Asian waters, suggests a northward biogeographic affinity for this region, possibly influenced by ocean currents (e.g., Kuroshio Current) in facilitating larval dispersal (Watanabe et al., 2009).

Central/Southern Luzon Province

The Central/Southern Luzon province encompasses a range of aquatic ecosystems, from the extensive lowland floodplains of the Central Luzon Basin to the volcanic lakes of the Batangas region. This province hosts some of the largest river systems in the Philippines, including the Pampanga and Pasig Rivers, which provide diverse habitats for freshwater fishes (Aquino et al., 2011).

The indicator species in Central/Southern Luzon reveal a mix of endemic freshwater species and those with marine affinities, offering insights into the region's unique ecological and evolutionary characteristics. The presence of the endemic *M. luzonensis* as an indicator species underscores the evolutionary uniqueness of this region's ichthyofauna, emphasizing the need for targeted conservation efforts to protect these endemic lineages. Strong indicators like *A. manillensis* and *L. plumbeus* suggest well-developed freshwater ecosystems, possibly with longer periods of isolation contributing to species divergence.

Greater Visayas Province

The Greater Visayas province is characterized by its fragmented geography, comprising numerous islands separated by narrow sea channels. This configuration results in a complex network of relatively small river systems and unique karst-associated aquatic habitats (Heaney et al., 2016).

The Greater Visayas province shows a highly diverse assemblage of indicator species, reflecting the complex geography of the central Philippines. The mix of marine (*O. polyophthalmus*, *C. puncticeps*), estuarine (*G. bicirrhosus*), and freshwater (*G. aureus*) species indicate a wide range of aquatic habitats, likely resulting from the fragmented nature of the Visayan islands. This diverse indicator assemblage supports the theory of island biogeography, with each island potentially harboring unique communities shaped by isolation and local adaptation. The presence of coral reef-associated species (e.g., *L. malabaricus*) as indicators suggests a strong interaction between reef and freshwater ecosystems, emphasizing the need for integrated coastal-freshwater management.

Factors contributing to the biogeographic distinctiveness of the Greater Visayas include island size and isolation as well as habitat diversity. The smaller size of individual islands and their degree of isolation influence species richness and endemism patterns, aligning with principles of island biogeography theory (MacArthur and Wilson, 1967). The presence of karst landscapes in regions like Samar and Leyte provides unique aquatic habitats, including underground rivers and sinkholes, which may support specialized fish assemblages (Bonacci et al., 2009).

Mindanao Province

The Mindanao province is distinguished by its large river systems, including the Rio Grande de Mindanao, and the presence of ancient lakes such as Lake Lanao. These features provide a diverse array of habitats and have likely played a crucial role in shaping the region's ichthyofauna (Herre, 1924; Escudero et al., 2013).

Mindanao's indicator species reflect its complex geological history and diverse habitats. The strong association with multiple Anguillidae species (*A. bicolor*, *A. borneensis*, *A. celebesensis*) suggests that Mindanao serves as an important habitat for eel populations in the region. This diversity may be influenced by Mindanao's proximity to the Celebes Sea and the complex ocean currents in the area, facilitating the dispersal of these catadromous species (Aoyama, 2009). Indicators like *C. macrocephalus* and *B. binotatus* point to well-developed freshwater ecosystems with possible influences from both Asian and Sundaic ichthyofaunas.

The mix of indicator species suggests that Mindanao may represent a biogeographic crossroads, with influences from the Sunda Shelf, Wallacea, and the oceanic Philippines. This aligns with the complex geological history of the island (Hall,

2002) and its position at the confluence of several biogeographic regions. The presence of Lake Lanao, an ancient lake which formerly harbors highly endemic cyprinid fauna, further underscores the unique evolutionary history of freshwater fishes in this province (Herre, 1924; Myers, 1960; Ismail et al., 2014).

Palawan-Mindoro Province

The Greater Palawan-Mindoro province stands out with its high number of indicator species and distinct faunal composition, offering valuable insights into its unique biogeographic history. This province encompasses the islands of Palawan, Calamianes, Mindoro, and surrounding smaller islands, which are geologically distinct from the rest of the Philippines.

The presence of multiple *Barbodes, Rasbora* and other primary freshwater fish species as indicators strongly support the Sundaic affinities of this region. This corroborates the geological history of Palawan and Mindoro as continental fragments derived from the Sunda Shelf (Blackburn et al., 2010). The high number of endemic indicators (e.g., *B. palavanensis*, *D. palawanensis*) suggests that this region has been a hotspot for *in situ* speciation, likely due to its long isolation and unique environmental conditions.

The diverse array of indicator species, including those specialized for different parts of the river continuum (e.g., *N. alestes* for upland streams, Gobiidae species for lower reaches), indicates a wide range of freshwater habitats. This habitat diversity, coupled with the region's complex geological history, has likely contributed to the high endemism and unique composition of the freshwater fish fauna in this province.

The biogeographic distinctiveness of the Palawan-Mindoro Province aligns with previous studies on other taxonomic groups, such as mammals and reptiles, which have also shown Sundaic affinities and high endemism in this region (Esselstyn et al., 2010;

Siler et al., 2012). This congruence across multiple taxonomic groups underscores the importance of this province as a distinct evolutionary region within the Philippines.

Patterns of Species Richness and Endemism

The variation in species richness across biogeographic provinces, with Central/Southern Luzon hosting the highest diversity, challenges the traditional expectation of higher species richness on larger islands like Mindanao. This pattern may be explained by several factors:

1. Habitat heterogeneity: The complex topography and diverse river systems of Central/Southern Luzon may provide a wider array of niches, supporting higher species richness (Rahel, 2007).

2. Historical stability: The region might have served as a refugium during past climatic fluctuations, allowing for the accumulation and persistence of species over time (Woodruff, 2010).

3. Sampling bias: The possibility that the observed patterns are influenced by differences in sampling effort across regions cannot be ruled out, a common challenge in biogeographic studies (Lomolino, 2004).

The high endemism observed in the Palawan-Mindoro province, as indicated by the CWE scores, underscores the evolutionary uniqueness of this region. This finding supports the recognition of Palawan as a distinct biogeographic unit, often referred to as the Palawan Micro-continent (Blackburn, 2015). The exceptional endemism in the Agus River/Lanao Lake catchment within Mindanao highlights the importance of ancient lakes as cradles of biodiversity, paralleling patterns observed in other ancient lake systems worldwide (Cristescu et al., 2010).

These patterns of species richness and endemism in freshwater fishes show both similarities and differences when compared to other taxonomic groups in the Philippines. For instance, the high endemism in Palawan-Mindoro aligns with patterns observed in birds and mammals (Brown et al., 2013), while the species richness peak in Central/Southern Luzon contrasts with some plant groups that show highest diversity in Mindanao (Cañedo-Argüelles et al., 2015a,b). These differences underscore the importance of taxon-specific analyses in understanding biodiversity patterns and highlight the unique contributions of freshwater fish data to Philippine biogeography.

Environmental Drivers of Fish Distribution

The GDM results provide valuable insights into the factors shaping freshwater fish distributions across the Philippines. The analysis reveals that the primary drivers of fish distribution patterns are current geographic distance and Pleistocene Aggregate Island Complexes (PAICs), rather than climate variables.

The significant role of PAICs in explaining distribution patterns (35% of variation) emphasizes the lasting impact of historical geography on contemporary biodiversity patterns. This finding strongly supports the PAIC hypothesis, which has been influential in explaining the distribution patterns of various taxa in Southeast Asia (Blackburn et al., 2015).

Geographic distance emerged as another crucial factor driving species turnover. This result supports the concept of distance decay in ecological communities, where similarity decreases with increasing geographic separation (Brown et al., 2013). In the context of freshwater fishes in an archipelagic setting, this pattern likely results from dispersal limitations. Marine barriers between islands pose significant obstacles to the movement of freshwater species, leading to increased differentiation between more distant populations.

Interestingly, the absence of climate variables as significant predictors in the GDM results is noteworthy. This finding contrasts with studies on other taxa or in different geographical contexts, where climate often plays a crucial role in shaping species distributions (Brown et al., 2013). The lack of climate signal in our analysis suggests that for freshwater fishes in the Philippines, historical factors (such as PAICs) and spatial processes (geographic distance) are more critical in determining distribution patterns.

This contrast with studies in continental tropical regions, where climate variables frequently emerge as dominant factors, underscores the unique biogeographic processes operating in insular systems. The strong influence of historical and spatial factors over contemporary climate conditions highlights the importance of considering historical biogeography and island biogeographic principles when studying insular freshwater systems.

Conservation Implications

The findings here have significant implications for freshwater fish conservation in the Philippines. The delineation of distinct biogeographic provinces provides a framework for identifying conservation priorities and managing fish biodiversity effectively. Recognizing these provinces as unique conservation units can guide targeted efforts to preserve the unique assemblages and evolutionary processes within each region.

In particular, the high endemism and distinct species assemblages in the Palawan-Mindoro Province underscore its conservation significance. This region should be prioritized for conservation actions, focusing on protecting its unique habitats and endemic species.

The Agus River/Lanao Lake catchment in Mindanao also emerges as a key area for conservation, given its high endemism and the presence of ancient lake ecosystems. Conservation efforts should prioritize the protection of these ancient lake systems, which are highly vulnerable to anthropogenic threats such as pollution, habitat destruction, and invasive species (Cohen et al., 1997). The conservation of ancient lakes is crucial not only for preserving endemic species but also for maintaining the unique evolutionary processes occurring in these ecosystems.

Additionally, the importance of geographic distance and PAICs in shaping fish distributions highlights the need for connectivity conservation strategies. Maintaining or restoring connectivity between river systems within and across islands can facilitate gene flow and support population resilience. Implementing measures to enhance connectivity, such as habitat corridors and fish passages, can mitigate the effects of habitat fragmentation and promote the persistence of freshwater fish populations.

Limitations and Future Directions

While this study provides a comprehensive analysis of freshwater fish biogeography in the Philippines, several limitations and areas for future research should be acknowledged. One significant limitation is the potential sampling gaps across different regions, as the dataset may not represent a uniform sampling effort. Future studies should focus on filling these gaps, particularly in understudied areas, to create a more complete picture of freshwater fish distribution and diversity. Additionally, this analysis offers only a snapshot of current distribution patterns, making long-term monitoring essential for understanding temporal dynamics and species' responses to environmental changes, such as climate change, habitat modification, and species introductions.

Incorporating functional trait data in future analyses could offer deeper insights into the ecological roles and potential ecosystem services provided by different fish assemblages. Understanding how functional traits are distributed across biogeographic provinces could enhance our knowledge of ecosystem functioning and resilience. Furthermore, integrating phylogenetic and population genetic data is crucial for elucidating the evolutionary history and connectivity of fish populations across the archipelago. Genetic analyses could identify cryptic species, uncover population structure, and reveal historical dispersal pathways, informing conservation strategies by highlighting genetically distinct populations that may require separate management.

Human impacts, such as land-use change, pollution, and overexploitation, are also critical factors that future research should incorporate to better understand their effects on fish distributions and inform management strategies. Assessing how these anthropogenic factors influence genetic diversity, and connectivity will be vital in developing effective conservation plans. Lastly, there is a need for integrated studies that combine freshwater fish data with other taxonomic groups to develop a more comprehensive understanding of Philippine biogeography. Comparative analyses could reveal shared biogeographic patterns or unique aspects of freshwater ecosystems that differ from terrestrial or marine systems, further enriching our understanding of biodiversity in the region.

Conclusion

In conclusion, this study provides the first comprehensive biogeographic analysis of freshwater fishes in the Philippine archipelago, revealing patterns that both align with and diverge from those observed in other taxonomic groups. By elucidating the complex interplay of historical, geographical, and environmental factors shaping fish distributions, this work contributes valuable insights to both theoretical biogeography and applied conservation. The unique perspective offered by freshwater fishes underscores the importance of taxon-specific analyses in understanding the full complexity of biodiversity patterns in archipelagic systems. As freshwater ecosystems face increasing threats from climate change, habitat loss, and overexploitation, this work provides a crucial foundation for developing effective, biogeographically informed conservation strategies to preserve the unique and irreplaceable freshwater fish biodiversity of the Philippines.

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Disclosure statement

The authors report there are no competing interests to declare.

Data availability statement

The data that support the findings of this study are available from the authors upon request.

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Table 1. List of freshwater fish biogeographic provinces in the Philippines and their corresponding branch length values, number of catchments, corrected weighted endemism (CWE) ranges, and observed species richness ranges.

Biogeographic Province	**# of catchments**	**Branch length**	**CWE**	**Observed Species Richness**
Northern Luzon	4	0.602	0.127-0.230	32-55
Central/Southern Luzon	9	0.502	0.095-0.191	24-105
Greater Visayas	7	0.502	0.120-0.181	34-98
Mindanao	8	0.54	0.088-0.388	25-75
Palawan-Mindoro	4	0.567	0.150-0.279	55-72

Table 2. Generalized dissimilarity models (GDM) for explaining the variation in freshwater fish diversity distribution pattern of the Philippines based on Environmental variables and PAIC groupings.

Category/Predictor	**Deviance explained (%)**	**Predictor Importance**	***p*-value**
Geography/Topography	38.50		
Geographic Distance		24.163	0.000
Catchment Area (km)		2.780	0.431
Mean Stream Length (km)		2.087	0.480
Basin Drainage Density		3.488	0.357
Average Catchment Slope		0.411	0.648
Mean Stream Slope		4.175	0.346
Mean Elevation (m)		10.270	0.200
Climate	9.72		
Annual rainfall (mm)		1.870	0.700
Max. Temperature		10.555	0.335
Mean Temperature		1.264	0.130
PAIC	35.00		
PAIC Groupings		40.575	0.00

Table 3. Indicator Species Analysis (IndVal) results for each biogeographic province.

Biogeographic Province	**Species**	**IndVal**	***p*-value**
Northern Luzon	*Anguilla japonica*	0.943	0.001
	Anguilla luzonensis	0.904	0.001
	Crenimugil crenilabis	0.849	0.001
	Crenimugil heterocheilos	0.770	0.002
	Lamnostoma taylori	0.598	0.034
	Mugil cephalus	0.707	0.003
	Oligolepis acutipennis	0.680	0.007
	Plicofollis magatensis	0.707	0.003
	Rhinogobius philippinus	0.737	0.005
	Rhinogobius tandikan	0.645	0.022
Central/Southern Luzon	*Arius dispar*	0.612	0.031
	Arius manillensis	0.837	0.001
	Gobiopterus brachypterus	0.632	0.011
	Leiopotherapon plumbeus	0.837	0.001
	Mistichthys luzonensis	0.632	0.021
	Nomorhamphus pectoralis	0.598	0.033
	Zenarchopterus philippinus	0.802	0.001
Greater Visayas	*Ambassis gymnocephalus*	0.650	0.039
	Cynoglossus puncticeps	0.840	0.001
	Dichotomyctere nigroviridis	0.698	0.036
	Glossogobius aureus	0.701	0.005
	Glossogobius bicirrhosus	0.845	0.001

	Hippichthys penicillus	0.665	0.013
	Lutjanus malabaricus	0.657	0.026
	Moringua raitaborua	0.756	0.004
	Ophichthus polyophthalmus	0.894	0.001
Mindanao	*Anguilla bicolor*	0.913	0.001
	Anguilla borneensis	0.707	0.001
	Anguilla celebesensis	0.744	0.038
	Barbodes binotatus	0.773	0.001
	Bathygobius fuscus	0.729	0.022
	Butis gymnopomus	0.624	0.013
	Clarias macrocephalus	0.833	0.002
	Lamnostoma orientale	0.598	0.032
	Redigobius chrysosoma	0.655	0.020
Greater Palawan-Mindoro	*Barbodes hemictenus*	0.577	0.039
	Barbodes palavanensis	0.577	0.034
	Dermogenys bispina	0.577	0.039
	Dermogenys palawanensis	0.577	0.034
	Dermogenys robertsi	0.577	0.034
	Eleutherochir opercularis	0.638	0.045
	Gobiosoma pallida	0.816	0.001
	Mangarinus waterousi	0.577	0.039
	Mugilogobius mertoni	0.624	0.020
	Nematabramis alestes	0.632	0.017
	Neostethus bicornis	0.707	0.003
	Pandaka trimaculata	0.577	0.039

	Periophthalmus malaccensis	0.577	0.036
	Pterocryptis taytayensis	0.577	0.033
	Rasbora argyrotaenia	0.816	0.001
	Rasbora everetti	0.577	0.033
	Rasbora lateristriata	0.577	0.034
	Rhinogobius estrellae	0.577	0.033
	Stiphodon palawanensis	0.577	0.034
	Tamanka siitensis	0.577	0.037

Figure 1. Map of the Philippines with elevations and catchment/river basin boundaries (in arrows) included in the analysis. Shades of blue indicate sea floor depth of 120 m (estimated sea level during the last glacial maximum, Pleistocene period). Letters designate Pleistocene Aggregate Island Complexes (PAIC) (e.g., Heaney, 1985; Brown et al., 2013; Robles, 2013) - A) Greater Luzon, B) Mindoro, C) Greater Panay-Negros, D) Greater Mindanao, E) Greater Palawan, and F) Greater Sulu Archipelago.

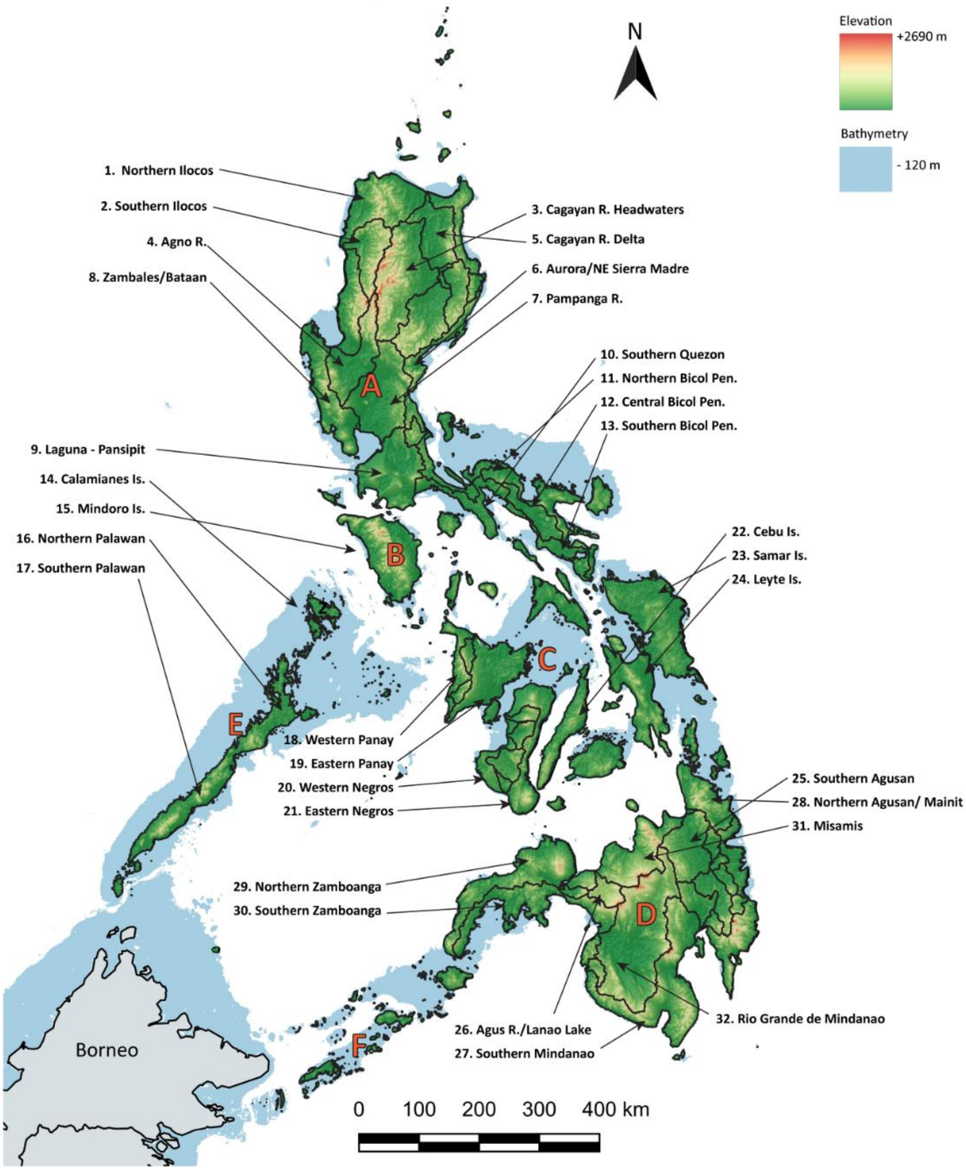

Figure 2. Map of the WPGMA tree based on Simpson's beta (βsim) dissimilarity matrix showing the proposed five freshwater fish biogeographic provinces in the Philippines.

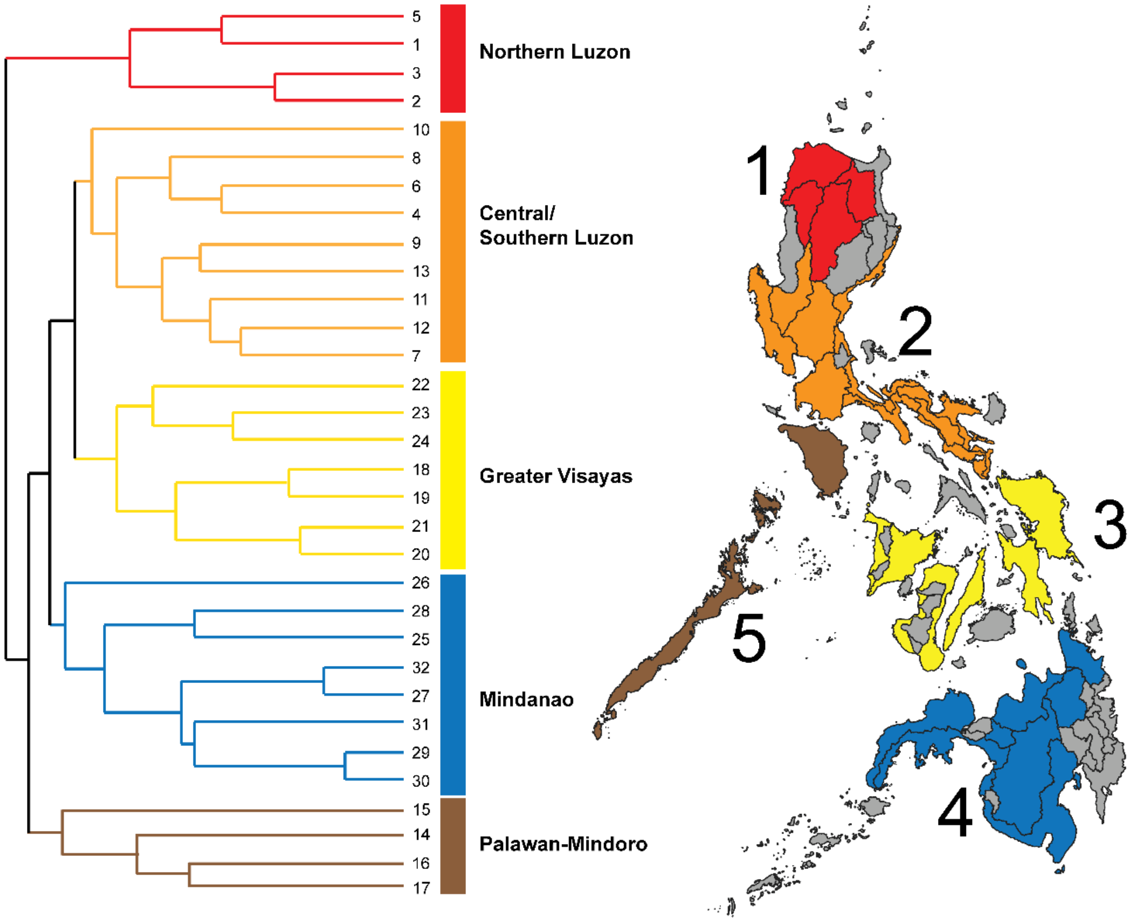

Figure 3. Corrected weighted endemism (A), and species richness (B) of freshwater fishes per catchment unit across the Philippines.

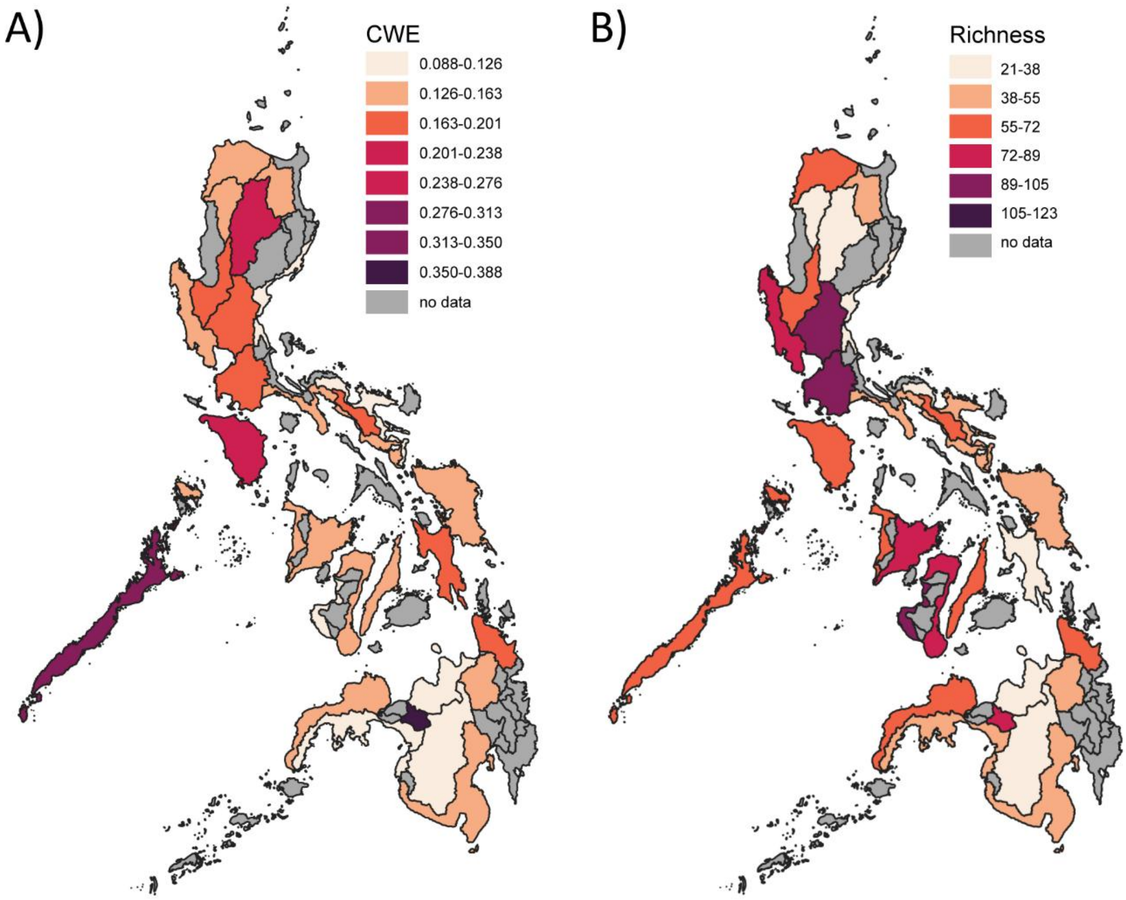

Figure 4. I-spline generated for the most significant environmental predictors (p-value <0.05) from the GDM analysis: Geographic Distance (x100km) and Pleistocene Aggregate Island Complex (PAIC) grouping.