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The Origins of Aquatic Biodiversity: Phylogenetic Patterns and Historical Biogeography

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Abstract The origins of aquatic biodiversity are shaped by complex phylogenetic patterns and historical biogeography. This study synthesizes findings from multiple studies to elucidate the evolutionary processes and biogeographic events that have contributed to the current diversity of aquatic species. Key factors include habitat-specific diversification rates, long-distance dispersal, vicariance, and the influence of ancient seaways. For instance, the diversification of marine and freshwater species is often linked to their ancestral habitats, with many marine species descending from marine ancestors and freshwater species from terrestrial ancestors. The biogeographic history of various aquatic taxa, such as syngnatharians and red seaweeds, highlights the role of ancient seas like the Tethys in shaping current distribution patterns through vicariance and dispersal events. Additionally, the evolutionary trajectories of freshwater fish genera in Southeast Asia and the Neotropical region underscore the importance of both colonization events and internal diversification in generating high levels of endemism and species richness. Overall, this study underscores the intricate interplay of phylogenetic and biogeographic factors in the origins of aquatic biodiversity, providing insights into the conservation of these vital ecosystems.

Keywords Aquatic biodiversity; Phylogenetic patterns; Historical biogeography; Vicariance; Long-distance dispersal

1 Introduction

Aquatic biodiversity encompasses the variety of life forms found in marine, freshwater, and estuarine ecosystems. These ecosystems are home to a vast array of species, each adapted to their unique environmental conditions. The distribution and richness of species in these habitats are influenced by a multitude of factors, including evolutionary history, ecological interactions, and environmental gradients. For instance, freshwater habitats, despite covering only a small fraction of the Earth's surface, exhibit high species richness and exceptional phylogenetic diversity (Román‐Palacios et al., 2022). Similarly, marine ecosystems, though expansive, show distinct patterns of biodiversity shaped by factors such as ocean currents and environmental selection (Ward et al., 2021).

Phylogenetic patterns provide insights into the evolutionary relationships among species and the historical processes that have shaped current biodiversity. By examining these patterns, researchers can infer the origins and diversification of species within different habitats. For example, studies have shown that most marine species are descended from marine ancestors, while many freshwater species have terrestrial origins (Román‐Palacios et al., 2022). Understanding these phylogenetic relationships is crucial for identifying the evolutionary pathways that have led to the current distribution of species and for predicting how biodiversity might respond to future environmental changes (Chen et al., 2018; Hammer et al., 2021).

Historical biogeography examines the distribution of species over time and the historical events that have influenced their current locations. This field of study is essential for understanding the processes of vicariance, dispersal, and extinction that have shaped the biogeographic patterns observed today. The biogeography of the freshwater fish family Anablepidae reveals how historical marine transgressions and ancient river connections have influenced their distribution (Frota et al., 2020). The diversity of freshwater macroinvertebrates in Neotropical streams is shaped by geographic isolation and local environmental factors (León et al., 2020).

The purpose of this study is to synthesize current knowledge on the origins of aquatic biodiversity, focusing on phylogenetic patterns and historical biogeography. By integrating findings from multiple studies, this study provides a comprehensive understanding of the evolutionary and biogeographic processes that have shaped aquatic biodiversity, and highlights the importance of both historical events and contemporary ecological factors in driving the diversity and distribution of aquatic species. This study will also identify gaps in current knowledge and suggest directions for future research to further elucidate the complex dynamics of aquatic biodiversity.

2 Phylogenetic Patterns in Aquatic Biodiversity

2.1 Methods of phylogenetic analysis

Phylogenetic analysis in aquatic biodiversity research often employs a combination of molecular and computational techniques to infer evolutionary relationships among species (Figure 1). Common methods include the use of multilocus datasets, which incorporate sequences from both nuclear and mitochondrial genes. For instance, in the study of coastal rove beetles, a multilocus dataset comprising DNA sequences from five nuclear genes (ArgK, CAD, EF1-α, wg, and 28S) and three mitochondrial genes (COI, COII, and 16S) was utilized to infer gene trees and species trees using both model-based (maximum likelihood and Bayesian) and parsimony-based methods (Song et al., 2018). Additionally, coalescent-based approaches, such as *BEAST analysis, are employed to resolve phylogenetic relationships and reconstruct time-calibrated phylogenies (Song et al., 2018).

The phylogenetic analysis by García-Girón et al. (2024) presents a comprehensive view of evolutionary relationships among key aquatic insect groups, using a vast dataset of 3125 gene sequences and 6038 nucleotide sites. The study achieves near-complete family-level coverage for stoneflies and caddisflies, and significant proportions for dragonflies, damselflies, and mayflies. The phylogenetic tree, detailed with colored lines indicating family extents and classification hypotheses, provides insight into monotypic families and polyphyletic assemblages. The inclusion of a time scale and palaeogeographical maps offers context for major evolutionary events. This work enhances the understanding of the diversification and biogeographical history of these aquatic insects, highlighting significant evolutionary patterns and divergence times within these aquatic lineages.

2.2 Major phylogenetic groups in aquatic environments

Aquatic environments host a diverse array of phylogenetic groups, each with unique evolutionary histories. Marine habitats, which cover approximately 70% of Earth's surface, are home to a variety of species descended from marine ancestors. In contrast, freshwater habitats, despite covering only 2% of Earth's surface, exhibit high species richness and exceptional phylogenetic diversity. Interestingly, most extant animal richness in freshwater is derived from terrestrial ancestors, highlighting the complex evolutionary transitions between habitats (Román‐Palacios et al., 2022). The study of coastal rove beetles further illustrates the diversity within specific clades, with species distributed along the eastern and western Palearctic and the western Nearctic coasts (Song et al., 2018).

2.3 Evolutionary relationships and divergence

The evolutionary relationships and divergence patterns among aquatic species are shaped by various historical and biogeographical factors. For example, the phylogenetic analysis of coastal rove beetles revealed that most divergence events occurred in the late Miocene and early Pliocene along the Pacific coasts. The East Asian seacoasts, in particular, harbored the most species-rich fauna within the ET clade (Song et al., 2018). Ancestral reconstructions of habitat indicate that marine species are predominantly descended from marine ancestors, while freshwater species often have terrestrial origins. This divergence is influenced by variation in diversification rates across different habitats (Román‐Palacios et al., 2022). The historical biogeography of these species is marked by dispersal and vicariance events, which have played significant roles in shaping their current distribution patterns (Song et al., 2018).

3 Historical Biogeography of Aquatic Species

3.1 Concepts and methods in historical biogeography

Historical biogeography aims to understand the distribution of species over time and space, integrating
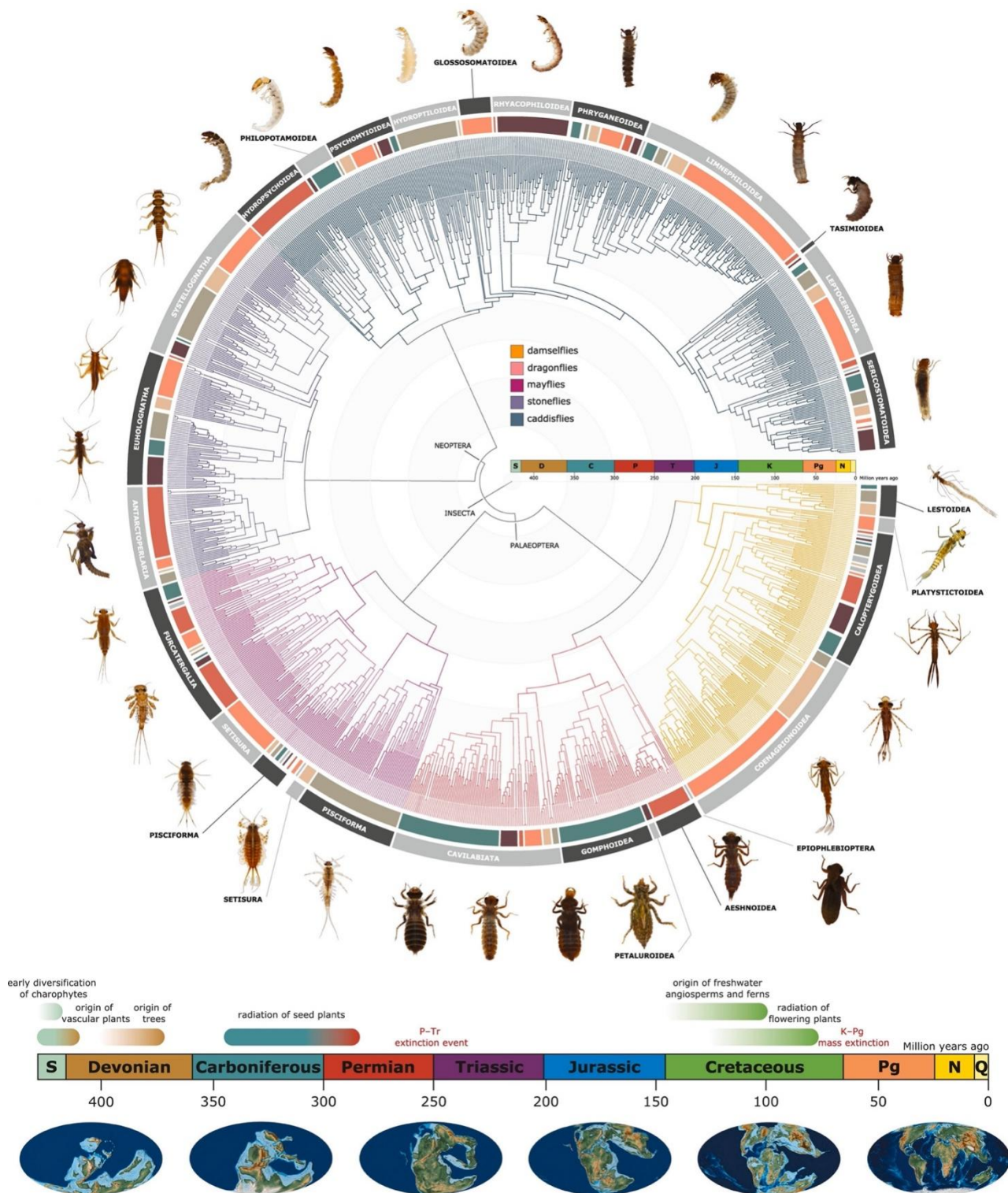
Figure 1 Time-calibrated phylogenetic tree of key groups of aquatic insects (Adopted from García-Girón et al., 2024)

Image caption: The tree is constructed from 3125 targeted rRNA and protein-coding gene sequences spanning nine loci and 6038 nucleotide sites. Colored lines in the tree's inner ring show the extent of each family as detailed in Supplementary Information Appendices S3−S6, while the outer ring depicts classification hypotheses for major insect lineages. Grey lines and white spaces in both rings indicate monotypic families or highly polyphyletic groups, respectively. The bottom of the figure features a time scale that aligns with significant palaeontological and geological events in Earth's history. Palaeogeographical reconstructions of the world's oceans and continents were created using GPlates ver. 2.3 and projected with the Mollweide equal-area cylindrical projection. Illustrations of insect larvae and nymphs were sourced from the Atlas of Common Freshwater Macroinvertebrates A more detailed view of this figure is available on Zenodo (see Data Availability) (Adapted from García-Girón et al., 2024)

phylogenetic data with geological and climatic history. Key methods include time-calibrated molecular phylogenies and ancestral range reconstruction. These approaches allow researchers to infer the historical distributions and diversification patterns of species. For instance, time-calibrated molecular phylogenies have been instrumental in examining the origins of coral reef fish biodiversity across the tropics, providing insights into the temporal patterns of marine endemism and tropical provinciality (Cowman et al., 2017). Similarly, the use of multi-gene datasets in phylogenetic studies has enabled the reconstruction of the historical biogeography of widely distributed groups like the Sciaenidae, revealing their origins and diversification patterns (Lo et al., 2015).

3.2 Historical distribution patterns
The distribution patterns of aquatic species are shaped by a combination of historical processes, including vicariance, dispersal, and extinction. In the case of tropical reef fishes, the Indo-Australian Archipelago (IAA) serves as a major biodiversity hotspot, characterized by a steep gradient in species richness from the center to the periphery of the Indo-Pacific region. This pattern is maintained by a mixture of paleo- and neo-endemic species, indicating multiple historical processes at play (Cowman et al., 2017). For the Sciaenidae family, ancestral range reconstruction suggests an origin in tropical America during the Oligocene to Early Miocene, followed by range expansions to the Eastern Atlantic and Indo-West Pacific, where the highest species richness is observed (Lo et al., 2015).

3.3 Major biogeographic events
Several major biogeographic events have significantly influenced the distribution and diversity of aquatic species (Figure 2). The formation of the IAA, for example, has been a critical factor in the genesis and maintenance of coral reef fish biodiversity. This region's complex geological history, including tectonic movements and sea-level changes, has created a dynamic environment for species diversification (Cowman et al., 2017). For the Sciaenidae, the transition between marine and euryhaline environments, as well as the occasional shift to freshwater habitats, highlights the role of habitat transitions in their biogeographic history. These transitions, coupled with fossil evidence, suggest that sciaenids first diversified in tropical America before expanding their range to other regions (Lo et al., 2015).

Cardoso et al. (2021) examines the phylogeny and biogeographic history of the *Hypostomus* catfish genus in the La Plata Basin. The time-calibrated phylogeny highlights significant evolutionary and dispersal events. Key geomorphological changes, including the *Michicola Arc* uplift (~30 Mya), river capture events, and Miocene marine transgressions, influenced species distribution and diversification. Using ancestral area reconstructions, the study traces Amazonian species' colonization routes into the La Plata Basin and their diversification. This integrated approach, combining phylogenetic and hydrogeological data, elucidates how orogenic and environmental changes shaped species evolution in the region.

By integrating phylogenetic diversity with ancestral biogeographic estimation, researchers can better understand how assemblage structures and biogeographic patterns have evolved over time, shedding light on the origins and maintenance of aquatic biodiversity hotspots.

4 Integration of Phylogenetics and Biogeography
4.1 Combined phylogenetic and biogeographic studies
Recent studies have demonstrated the power of integrating phylogenetic and biogeographic data to uncover the origins and maintenance of biodiversity in various aquatic habitats. For instance, a study on global biodiversity across land, sea, and freshwater habitats revealed that the relative richness of these habitats is closely related to variations in diversification rates. Ancestral reconstructions indicated that most marine species are descended from marine ancestors, while most terrestrial species originated from freshwater ancestors. Interestingly, the majority of extant animal richness in freshwater is derived from terrestrial ancestors, underscoring the complex evolutionary transitions between habitats (Román‐Palacios et al., 2022).
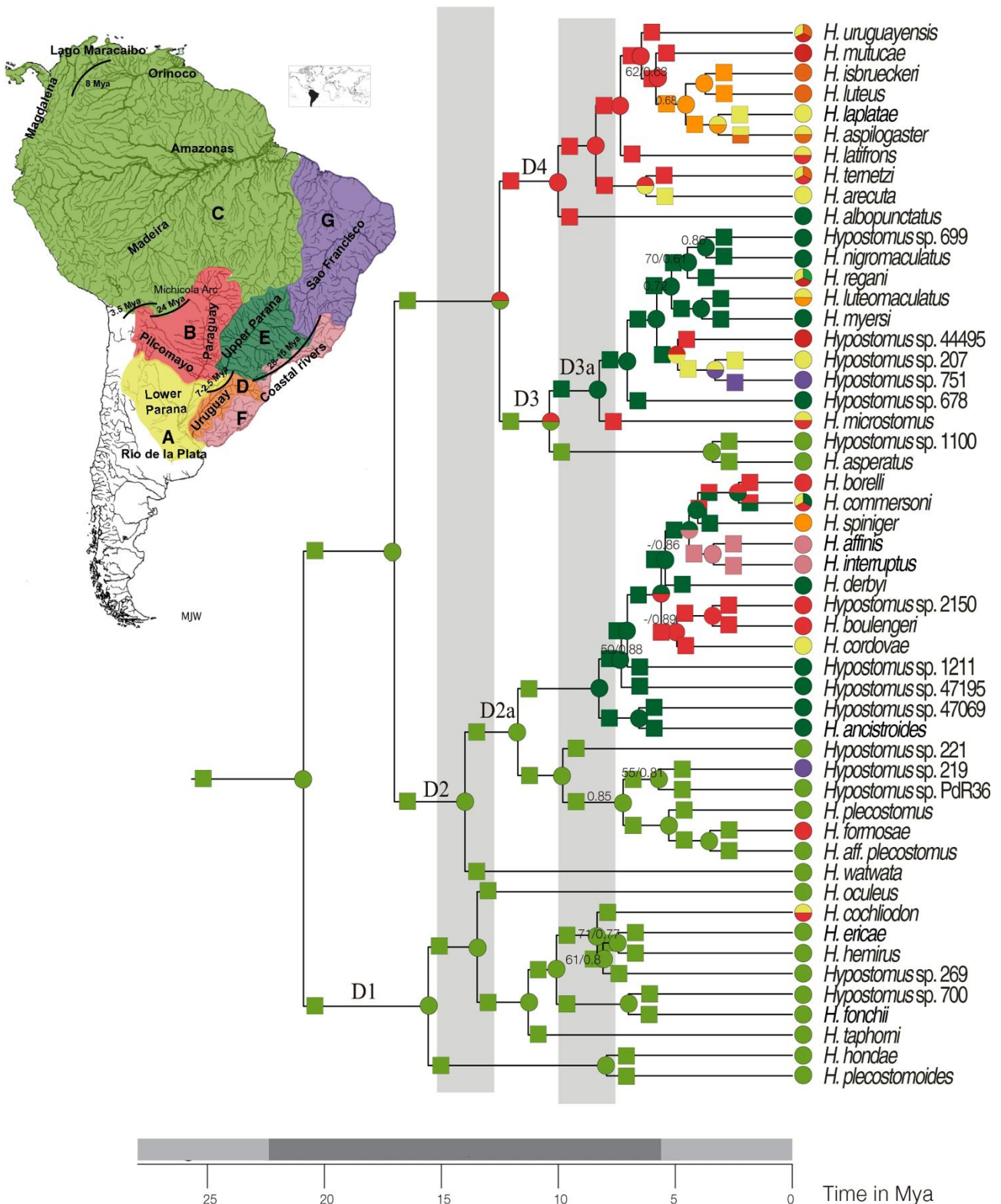
Figure 2 Time-calibrated multilocus phylogeny for the *Hypostomus* genus based on hydrogeological calibration points, including ancestral area reconstructions obtained using RevBayes (Adopted from Cardoso et al., 2021)

Image caption: For the ecoregion codes and the D1–D4 clades, see text. Grey vertical bars are the maximum flooding events of the Miocene Marine ingression. Values in nodes show bootstrap supports lower than 80% and posterior probabilities supports lower than 0.9 performed in RaxML and MrBayes reconstructions, respectively. For the posterior probabilities of ancestral area reconstructions see Fig. S4. Map was created in CorelDRAW Graphics Suite 2020 version 22.1.0.517 (Adopted from Cardoso et al., 2021)

In the context of marine biodiversity, particularly tropical reef fishes, the integration of time-calibrated molecular phylogenies with ancestral biogeographic estimates has provided a framework to examine the origins of coral reef fish biodiversity. This approach has highlighted temporal patterns of marine endemism and tropical provinciality, revealing that the Indo-Australian Archipelago (IAA) serves as a major biodiversity hotspot. The study found that the IAA's biodiversity is maintained by a mixture of paleo- and neo-endemic fishes, suggesting multiple historical processes at play. Enhanced precision in sampling geographic ranges has allowed for the division of discrete realms, regions, and provinces, further elucidating the biogeographic patterns of reef fishes (Cowman et al., 2017).

These combined phylogenetic and biogeographic studies underscore the importance of integrating multiple data sources to understand the complex history of aquatic biodiversity. By doing so, researchers can better identify the processes driving species diversification and distribution, ultimately aiding in the conservation of these diverse ecosystems.

4.2 Case studies of integrated approaches

One notable case study involves the examination of global biodiversity across land, sea, and freshwater habitats. This study revealed that most plant and animal species are terrestrial, despite terrestrial habitats covering only about 28% of Earth's surface. Marine habitats, which cover approximately 70% of the Earth's surface, have fewer species, while freshwater habitats, despite their tiny area (2%), exhibit relatively high species richness and exceptional phylogenetic diversity. The study found that the relative richness of these habitats is related to variation in diversification rates. Ancestral reconstructions indicated that most marine species are descended from marine ancestors, and most terrestrial species from freshwater ancestors. Interestingly, most extant animal richness in freshwater is derived from terrestrial ancestors, highlighting the complex evolutionary history of these habitats (Román‐Palacios et al., 2022).

Another case study focuses on the biogeography of tropical reef fishes, particularly within the Indo-Australian Archipelago (IAA), the largest marine biodiversity hotspot. This region exhibits complex patterns of endemism and species richness gradients. Time-calibrated molecular phylogenies and ancestral biogeographic estimates have been used to examine the origins of coral reef fish biodiversity. The study highlighted that the IAA contains a mixture of paleo- and neo-endemic fishes, suggesting multiple historical processes involved in the origin and maintenance of this biodiversity hotspot. The integration of phylogenetic diversity with ancestral biogeographic estimation has allowed for a more precise division of discrete realms, regions, and provinces across the tropics, enhancing our understanding of tropical provinciality and assemblage structure changes over time (Cowman et al., 2017).

4.3 Insights from integrative analyses

Integrative analyses combining phylogenetics and biogeography have provided several key insights into the origins and distribution of aquatic biodiversity. Firstly, these analyses have underscored the importance of historical biogeographic events, such as vicariance and dispersal, in shaping current biodiversity patterns. For instance, the high species richness in freshwater habitats, despite their limited area, can be attributed to historical colonization events from terrestrial ancestors, followed by subsequent diversification (Román‐Palacios et al., 2022).

Secondly, the integration of phylogenetic and biogeographic data has revealed the dynamic nature of biodiversity hotspots. The IAA, for example, has been shown to be a region of both species creation and demise, with a complex history of endemism and species turnover. This highlights the role of both historical and contemporary processes in maintaining biodiversity in these regions (Cowman et al., 2017).

Lastly, these integrative approaches have emphasized the need for comprehensive sampling and precise geographic range data to accurately reconstruct the evolutionary history of species. Improved sampling and data integration have led to more refined biogeographic classifications and a better understanding of the temporal and spatial dynamics of biodiversity (Cowman et al., 2017).

In conclusion, the integration of phylogenetics and biogeography has been instrumental in uncovering the historical and evolutionary processes that have shaped aquatic biodiversity. These integrative approaches continue to provide valuable insights into the origins, maintenance, and distribution of species across different habitats, contributing to our broader understanding of biodiversity patterns on Earth.

5 Evolutionary Mechanisms Underlying Aquatic Biodiversity

5.1 Speciation processes

Speciation, the process by which new species arise, is a fundamental mechanism driving aquatic biodiversity. In freshwater environments, speciation can be influenced by various factors, including geographic isolation and ecological differentiation. For instance, the parallel speciation of freshwater forms from ancestral amphidromous forms in *Rhinogobius* goby fish across the Ryukyu Archipelago, highlighting the role of ecosystem size in predicting speciation probability (Prates and Singhal, 2020). Additionally, the Amazon basin's diverse ecological conditions, such as differences in water types, can drive speciation through local adaptations in sensory systems, which affect interbreeding chances between populations (Borghezan et al., 2021).

5.2 Adaptive radiation

Adaptive radiation, where a single ancestral species rapidly diversifies into multiple new species, each adapted to a different ecological niche, is another key mechanism. The Amazon's high freshwater organism richness is a prime example, where distinct water types (black, white, and clear) create varied ecological niches that drive the evolution of sensory systems and contribute to fish diversity (Borghezan et al., 2021). Similarly, the historical biogeography of cycads, which expanded from Laurasian origins to Gondwana, showcases how adaptive radiation can lead to significant biodiversity through vicariance and niche differentiation over geological timescales (Coiro et al., 2023).

5.3 Environmental and ecological drivers

Environmental and ecological factors play crucial roles in shaping aquatic biodiversity. Temperature, for instance, has been identified as a significant driver of fungal community composition in freshwater streams, with thermal preferences influencing biodiversity patterns along latitudinal gradients (Seena et al., 2019). In marine environments, environmental conditions such as temperature and anthropogenic stressors like pollution and fishing pressure have been shown to influence the biogeographic patterns of metazoans, protists, and bacteria (Holman et al., 2021). Furthermore, in Lake Lugu, water depth and associated abiotic variables significantly affect the biomass, species richness, and community composition of bacteria, diatoms, and chironomids, demonstrating the importance of both abiotic and biotic interactions in structuring aquatic communities (Zhao et al., 2019).

In summary, the evolutionary mechanisms underlying aquatic biodiversity are multifaceted, involving speciation processes driven by geographic and ecological factors, adaptive radiation in response to diverse ecological niches, and environmental drivers that shape community composition and species richness across different aquatic habitats. Understanding these mechanisms is crucial for conserving aquatic biodiversity in the face of ongoing environmental changes.

6 Fossil Record and Molecular Data

6.1 Contributions of the fossil record

The fossil record provides critical insights into the origins and diversification of aquatic biodiversity. Fossil evidence reveals the historical biogeography and phylogenetic patterns of various aquatic species, offering a temporal framework to understand how current biodiversity patterns have evolved (Figure 2). For instance, the study of tropical reef fishes highlights the importance of fossil data in identifying areas of species creation and demise, particularly in biodiversity hotspots like the Indo-Australian Archipelago (IAA) (Cowman et al., 2017). Fossils help trace the lineage of species, revealing the historical processes that have shaped current biodiversity distributions. This historical perspective is essential for understanding the long-term dynamics of species richness and endemism in marine environments.
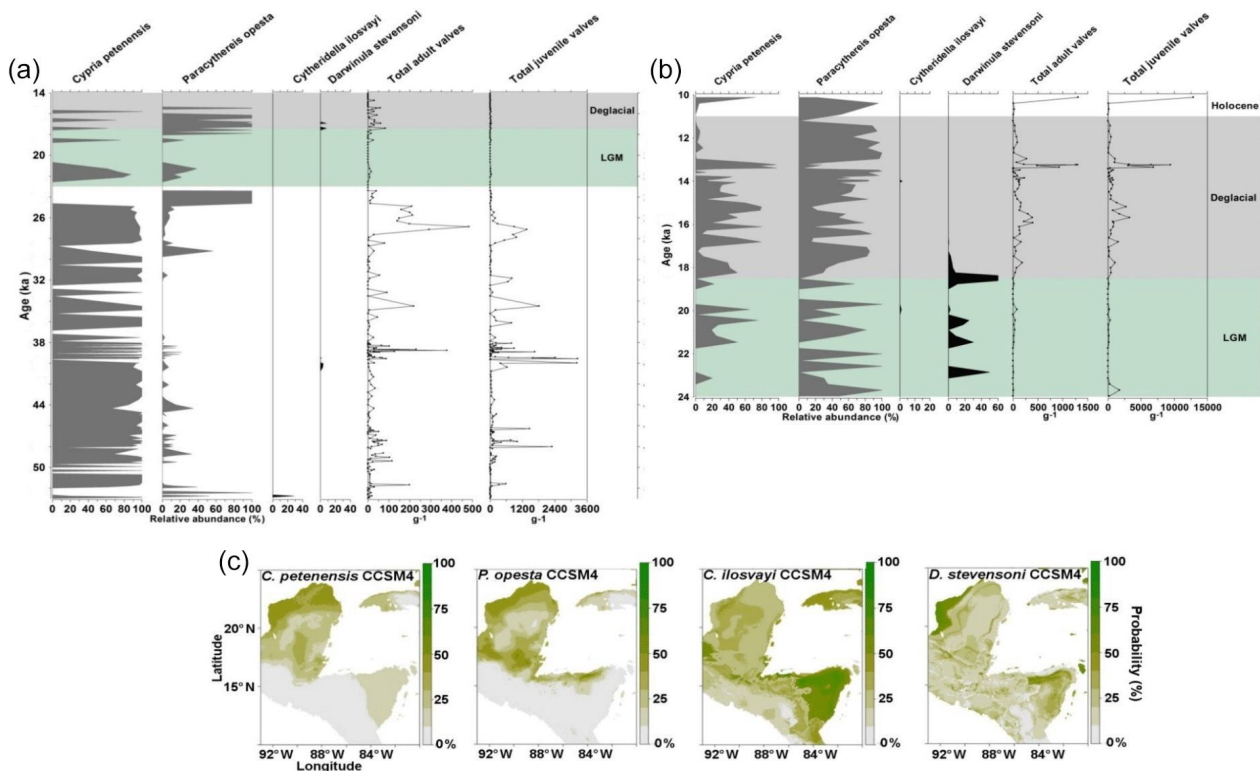
Figure 2 Fossil record of the period 53-10 and species niche modelling results for the last ~22 kyr (representing last glacial maximum climate) for four ostracode species: *Cypria petenensis*, *Paracythereis opesta*, *Cytheridella ilosvayi* and *Darwinula stevensoni* (Adopted from Cohuo et al., 2020)

Image caption: Fossil ostracode record from Lake Petén Itzá (a) Core PI-2 for the period 53-14 ka, (b) core PI-6 for the period 24-10 ka and (c) map showing the probability of species distributions based on the CCSM4 climate model (Adopted from Cohuo et al., 2020)

Cohuo et al. (2020) investigates the fossil records and species distribution models of four ostracode species from Lake Petén Itzá, focusing on periods spanning the last interglacial and glacial epochs. The analysis reveals that these species, particularly *Cypria petenensis*, exhibited varying abundance and relative frequencies, with notable occurrences aligning with significant climatic events. The complementary patterns observed between cores PI-2 and PI-6 suggest a resilient presence of endemic species during both the Last Glacial Maximum (LGM) and subsequent deglacial periods. Species distribution models, informed by the CCSM4 climate model, underscore the adaptability of these organisms to historical climate fluctuations. This research enhances our understanding of past biodiversity and the ecological responses of aquatic species to environmental changes in the region.

6.2 Molecular phylogenetics and genomics
Molecular phylogenetics and genomics have revolutionized our understanding of aquatic biodiversity by providing detailed insights into the evolutionary relationships among species. Time-calibrated molecular phylogenies, coupled with ancestral biogeographic estimates, have been instrumental in examining the origins of coral reef fish biodiversity across the tropics (Cowman et al., 2017). These methods allow researchers to reconstruct the evolutionary history of species, identifying key diversification events and ancestral habitats. For example, molecular data have shown that most marine species are descended from marine ancestors, while most terrestrial species have freshwater origins (Román‐Palacios et al., 2022). This molecular evidence complements fossil data, offering a more comprehensive view of the evolutionary processes driving aquatic biodiversity.

6.3 Integrating fossil and molecular evidence
Integrating fossil and molecular evidence provides a holistic approach to studying the origins of aquatic biodiversity. By combining these data sources, researchers can cross-validate findings and gain a more nuanced

understanding of historical biogeography and phylogenetic patterns. The integration of phylogenetic diversity with ancestral biogeographic estimation has shown how assemblage structure and tropical provinciality have changed over time, particularly in marine environments (Cowman et al., 2017). This combined approach helps to identify the relative contributions of historical and contemporary processes in shaping current biodiversity patterns. For instance, the high phylogenetic diversity in freshwater habitats, despite their small area, underscores the importance of both fossil and molecular data in revealing the complex evolutionary history of these ecosystems (Román‑Palacios et al., 2022).

The contributions of the fossil record, molecular phylogenetics, and the integration of these data sources are crucial for understanding the origins and maintenance of aquatic biodiversity. These approaches provide complementary insights that enhance our knowledge of the evolutionary and biogeographic processes shaping the diversity of life in aquatic environments.

7 Biogeographic Patterns in Different Aquatic Systems

7.1 Freshwater ecosystems

Freshwater ecosystems, despite covering only about 2% of the Earth's surface, exhibit a remarkable level of species richness and phylogenetic diversity. This high biodiversity is largely attributed to the unique evolutionary histories and diversification rates of species inhabiting these environments. Freshwater habitats have been shown to harbor a significant number of species that are derived from terrestrial ancestors, highlighting a complex biogeographic history where terrestrial lineages have repeatedly colonized freshwater systems (Román‑Palacios et al., 2022). The conservation importance of these habitats is underscored by their exceptional biodiversity, which is often overlooked in broader biodiversity studies that tend to focus on terrestrial and marine environments (Román‑Palacios et al., 2022).

7.2 Marine ecosystems

Marine ecosystems, which cover approximately 70% of the Earth's surface, display a different pattern of biodiversity compared to freshwater systems. The largest marine biodiversity hotspot is located in the Indo-Australian Archipelago (IAA), driven primarily by taxa associated with tropical coral reefs. This region forms a 'bullseye' of species richness, with a steep gradient extending to the periphery of the Indo-Pacific region (Cowman et al., 2017). The biogeographic patterns in marine ecosystems are shaped by a combination of paleo- and neo-endemic species, indicating multiple historical processes that have contributed to the current biodiversity. Time-calibrated molecular phylogenies and ancestral biogeographic estimates have been instrumental in understanding the origins and maintenance of coral reef fish biodiversity, revealing complex patterns of endemism and provinciality (Cowman et al., 2017).

7.3 Transitional and brackish water ecosystems

Transitional and brackish water ecosystems, such as estuaries and mangroves, represent unique biogeographic zones where freshwater and marine influences converge. These ecosystems often serve as critical habitats for a variety of species that are adapted to fluctuating salinity levels. The biogeographic patterns in these systems are influenced by the dynamic interactions between freshwater and marine species, leading to unique assemblages that are distinct from those found in purely freshwater or marine environments. The evolutionary histories of species in transitional ecosystems are shaped by their ability to adapt to varying salinity conditions, which can drive speciation and contribute to the overall biodiversity of these habitats.

The biogeographic patterns in different aquatic systems are shaped by a combination of historical biogeography, phylogenetic diversity, and ecological factors. Freshwater ecosystems exhibit high species richness derived from terrestrial ancestors, marine ecosystems are characterized by complex patterns of endemism and provinciality, and transitional ecosystems represent unique zones of biodiversity influenced by both freshwater and marine species. Understanding these patterns is crucial for the conservation and management of aquatic biodiversity across different habitats.

8 Conservation Implications

8.1 Phylogenetic diversity and conservation

Phylogenetic diversity (PD) is a crucial aspect of biodiversity that reflects the evolutionary history and relationships among species. It provides insights into the conservation value of different habitats by highlighting areas with unique evolutionary lineages. Freshwater habitats, despite their small area, exhibit exceptional phylogenetic diversity. This is largely due to the high diversification rates and the unique evolutionary histories of species that have adapted to these environments. The conservation importance of freshwater habitats is underscored by their high phylogenetic diversity, which is derived from both marine and terrestrial ancestors (Román‐Palacios et al., 2022). In marine environments, particularly tropical coral reefs, the integration of phylogenetic diversity with ancestral biogeographic data has revealed complex patterns of endemism and provinciality. These patterns are essential for understanding the origins and maintenance of biodiversity hotspots, such as the Indo-Australian Archipelago (IAA) (Cowman et al., 2017).

8.2 Conservation planning of historical biogeography

Historical biogeography plays a pivotal role in conservation planning by providing a temporal and spatial framework to understand the distribution of biodiversity. The origins of biodiversity in different habitats, such as terrestrial, marine, and freshwater, are influenced by historical processes that have shaped current species distributions. For instance, the high species richness in freshwater habitats is linked to their historical connections with terrestrial environments, while marine species richness is often derived from marine ancestors (Román‐Palacios et al., 2022). In the context of tropical coral reefs, the biogeographic history of reef fishes has been elucidated through time-calibrated molecular phylogenies and ancestral biogeographic estimates. These studies have identified areas of species creation and demise, which are critical for developing effective conservation strategies (Cowman et al., 2017). By integrating phylogenetic and biogeographic data, conservation planning can prioritize regions with unique evolutionary histories and high biodiversity, ensuring the protection of both current and future biodiversity.

8.3 Case studies in conservation strategies

Case studies in conservation strategies highlight the application of phylogenetic and biogeographic data in real-world scenarios. Freshwater habitats, for example, have been identified as critical conservation targets due to their high phylogenetic diversity and unique evolutionary lineages. Conservation efforts in these habitats can benefit from understanding the historical biogeography that has led to their current biodiversity patterns (Román‐Palacios et al., 2022). In marine environments, particularly tropical coral reefs, conservation strategies have been informed by the integration of phylogenetic diversity and ancestral biogeographic data. The IAA, as a major marine biodiversity hotspot, has been a focal point for such studies. The identification of paleo- and neo-endemic fishes in this region has provided insights into the historical processes that have shaped its biodiversity. These findings are essential for developing targeted conservation strategies that address both the protection of existing species and the preservation of evolutionary processes that generate biodiversity (Cowman et al., 2017). By examining these case studies, it becomes evident that a comprehensive understanding of phylogenetic diversity and historical biogeography is crucial for effective conservation planning and the long-term preservation of biodiversity.

9 Challenges and Future Directions

9.1 Methodological challenges

The study of aquatic biodiversity origins and patterns is fraught with several methodological challenges. One significant issue is the under-sampling of certain taxa, particularly endemic species, which can obscure our understanding of biodiversity genesis and maintenance. For instance, the biogeography of tropical reef fishes has been complicated by the under-sampling of endemic fishes in phylogenetic studies, leading to incomplete data on species creation and demise in biodiversity hotspots like the Indo-Australian Archipelago (IAA) (Cowman et al., 2017). Additionally, the integration of phylogenetic relatedness and ancestral biogeography into metrics for defining discrete realms, regions, and provinces is still in its nascent stages, further complicating the analysis (Cowman et al., 2017).

Another challenge is the accurate reconstruction of historical biogeography and diversification patterns. For example, the study of the Sciaenidae family revealed repeated habitat transitions between marine and euryhaline environments, but complete transitions to freshwater occurred only a few times, making it difficult to generalize findings across different taxa (Lo et al., 2015). The reliance on molecular phylogenetic frameworks and fossil evidence also introduces uncertainties, as these methods can sometimes yield conflicting results or lack the resolution needed for fine-scale biogeographic reconstructions (Lo et al., 2015).

9.2 Research gaps and opportunities

Despite the progress made, several research gaps remain that present opportunities for future studies. One notable gap is the limited understanding of the origins of biodiversity in freshwater habitats, which, despite their small area, exhibit high species richness and exceptional phylogenetic diversity (Román‐Palacios et al., 2022). Further research is needed to elucidate the evolutionary processes that have led to such high diversity in these habitats and to understand the conservation importance of freshwater ecosystems (Román‐Palacios et al., 2022).

Another area ripe for exploration is the temporal patterns of marine endemism and tropical provinciality. The current understanding is based on time-calibrated molecular phylogenies and ancestral biogeographic estimates, but increased precision and sampling of geographic ranges are needed to refine these patterns. This could help in identifying areas of species creation and demise more accurately and in understanding the multiple historical processes involved in the origin and maintenance of marine biodiversity hotspot.

9.3 Emerging trends and innovations

Emerging trends and innovations in the study of aquatic biodiversity are promising and could address some of the existing challenges. Advances in molecular techniques and genomic data are providing more detailed and accurate phylogenetic trees, which can improve our understanding of species diversification and biogeographic patterns. For example, the use of multi-gene datasets has allowed for a more comprehensive reconstruction of the historical biogeography of the Sciaenidae family, revealing previously unrecognized lineages and complex habitat transitions.

Additionally, the integration of ecological and evolutionary data is becoming increasingly important. Studies that combine phylogenetic diversity with ancestral biogeographic estimation are beginning to show how assemblage structures and tropical provinciality have changed over time, offering new insights into the dynamics of biodiversity. These integrative approaches are likely to become more prevalent, providing a more holistic understanding of the origins and maintenance of aquatic biodiversity.

While significant methodological challenges and research gaps remain, the field of aquatic biodiversity is poised for exciting advancements. By leveraging emerging trends and innovations, researchers can continue to unravel the complex phylogenetic patterns and historical biogeography that underpin the rich diversity of life in aquatic environments.

10 Concluding Remarks

The study of aquatic biodiversity has uncovered complex patterns influenced by phylogenetic and biogeographic processes, as revealed by extensive literature reviews. Key findings emphasize habitat-specific richness, with terrestrial habitats, despite covering only 28% of Earth's surface, hosting the majority of species. In contrast, marine habitats cover 70% of the planet but have fewer species, while freshwater habitats show high richness and exceptional phylogenetic diversity despite covering just 2% of the surface. The South American freshwater ichthyofauna, enriched by marine-derived lineages, reflects historical biogeographic patterns shaped by vicariance, dispersal, and extinction events. Additionally, elevational gradients impact bacterial diversity, with local environmental factors playing a crucial role. The biogeographic history of eelpouts suggests that speciation and dispersal within areas are key, with minimal evidence that ocean cooling affects diversification. Cross-kingdom biogeographic structures are consistently driven by environmental conditions and anthropogenic stressors among marine metazoans, protists, and bacteria.

The study also highlights the importance of integrating phylogenetics with biogeography to understand the origins and maintenance of aquatic biodiversity. Phylogenetic analyses shed light on evolutionary relationships and historical processes, while biogeographic studies show how species distributions are influenced by both historical and contemporary environmental factors. This integration helps elucidate mechanisms behind speciation, diversification, and extinction, providing a comprehensive view of biodiversity patterns across various habitats and taxonomic groups.

Looking forward, future research should focus on enhancing phylogenetic resolution with genome-wide data, conducting studies across elevational and latitudinal gradients, and investigating biogeographic patterns across multiple taxonomic groups. It is also vital to integrate historical and contemporary factors to better understand species distributions and apply these insights to conservation strategies, especially in regions facing significant anthropogenic pressures. These efforts are crucial for developing a deeper understanding of the origins and dynamics of aquatic biodiversity and enhancing conservation and management strategies.

Conflict of Interest Disclosure
The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

Reference
Borghezan E.D.A., Pires T.H.D.S., Ikeda T., Zuanon J., and Kohshima S., 2021, A review on fish sensory systems and amazon water types with implications to biodiversity, Frontiers in Ecology and Evolution, 8: 589760.
https://doi.org/10.3389/fevo.2020.589760

Cardoso Y P Jardim de Queiroz L Bahechar I A et al, Multilocus phylogeny and historical biogeography of Hypostomus shed light on the processes of fish diversification in La Plata Basin, Scientific Reports, 11(1): 5073.

Chen I., Nishida S., Chou L., Tajima Y., Yang W., Isobe T., Yamada T., Hartman K., and Hoelzel A., 2018, Concordance between genetic diversity and marine biogeography in a highly mobile marine mammal the Risso's dolphin, Journal of Biogeography, 45: 2092 - 2103.
https://doi.org/10.1111/jbi.13360

Cohuo S., Macario-González L., Wagner S., Naumann K., Echeverría-Galindo P., Pérez L., Curtis J., Brenner M., and Schwalb A., Influence of late Quaternary climate on the biogeography of Neotropical aquatic species as reflected by non-marine ostracodes, Biogeosciences, 17(1): 145-161.

Coiro M., Allio R., Mazet N., Seyfullah L., and Condamine F., 2023, Reconciling fossils with phylogenies reveals the origin and macroevolutionary processes explaining the global cycad biodiversity, The New Phytologist, 240(4): 1616-1635.
https://doi.org/10.1111/nph.19010

Cowman P., Parravicini V., Kulbicki M., and Floeter S., 2017, The biogeography of tropical reef fishes: endemism and provinciality through time, Biological Reviews, 92(4): 2112-2130.
https://doi.org/10.1111/brv.12323

Frota A., Morrone J.J., and Graça W.J., 2020, Evolutionary biogeography of the freshwater fish family Anablepidae (Teleostei: Cyprinodontiformes) a marine-derived Neotropical lineage, Organisms Diversity and Evolution, 20(3): 439-449.
https://doi.org/10.1007/s13127-020-00444-1

García-Girón J., Múrria C., Arnedo M.A., Bonada N., Cañedo-Argüelles M., Derka T., Fernández-Calero J.M., Li Z.F., de Figueroa J.M.T., Xie Z.C., and Heino J., 2024, A time-calibrated 'Tree of Life'of aquatic insects for knitting historical patterns of evolution and measuring extant phylogenetic biodiversity across the world, Earth-Science Reviews, 2024: 104767.

Hammer M.P., Adams M., Unmack P.J., Hassell K.L., and Bertozzi T., 2021, Surprising Pseudogobius: molecular systematics of benthic gobies reveals new insights into estuarine biodiversity (Teleostei: Gobiiformes), Molecular Phylogenetics and Evolution, 160: 107140.
https://doi.org/10.1016/j.ympev.2021.107140

Holman L.E., Bruyn M., Creer S., Carvalho G., Robidart J., and Rius M., 2021, Animals protists and bacteria share marine biogeographic patterns, Nature Ecology and Evolution, 5(6): 738-746.
https://doi.org/10.1038/s41559-021-01439-7

León L.F., Cornejo A., Gavilán R.G., and Aguilar C., 2020, Hidden biodiversity in Neotropical streams: DNA barcoding uncovers high endemicity of freshwater macroinvertebrates at small spatial scales, PLoS ONE, 15(8): e0231683.
https://doi.org/10.1371/journal.pone.0231683

Lo P.C., Liu S.H., Chao N.L., Nunoo F.K., Mok H.K., and Chen W.J., 2015, A multi-gene dataset reveals a tropical New World origin and Early Miocene diversification of croakers (Perciformes: Sciaenidae), Molecular Phylogenetics and Evolution, 88: 132-43 .

https://doi.org/10.1016/j.ympev.2015.03.025

Prates I., and Singhal S., 2020, Predicting speciation probability from replicated population histories, Molecular Ecology, 29: 2954-2956, https://doi.org/10.1111/mec.15577

Román‑Palacios C., Moraga-López D., and Wiens J.J., 2022, The origins of global biodiversity on land sea and freshwater, Ecology Letters, 25(6): 1376-1386. https://doi.org/10.1111/ele.13999

Seena S., Bärlocher F., Sobral O., Gessner M., Dudgeon D., Mckie B., Chauvet É., Boyero L., Ferreira V., Frainer A., Bruder A., Matthaei C., Fenoglio S., Sridhar K., Albariño R., Douglas M., Encalada A., García E., Ghate S., Giling D., Gonçalves V., Iwata T., Landeira-Dabarca A., McMaster D., Medeiros A., Naggea J., Pozo J., Raposeiro P., Swan C., Tenkiano N., Yule C., and Graça M.A., 2019, Biodiversity of leaf litter fungi in streams along a latitudinal gradient, The Science of the Total Environment, 661: 306-315. https://doi.org/10.1016/j.scitotenv.2019.01.122

Song J., and Ahn K., 2018, Species trees temporal divergence and historical biogeography of coastal rove beetles (Coleoptera: Staphylinidae) reveal their early Miocene origin and show that most divergence events occurred in the early Pliocene along the Pacific coasts, Cladistics 34, https://doi.org/10.1111/cla.12206

Ward B., Cael B., Collins S., and Young C., 2021, Selective constraints on global plankton dispersal, Proceedings of the National Academy of Sciences of the United States of America, 118(10): e2007388118. https://doi.org/10.1073/pnas.2007388118

Zhao W., Hu A., Ni Z., Wang Q., Zhang E., Yang X., Dong H., Shen J., Zhu L., and Wang J., 2019, Biodiversity patterns across taxonomic groups along a lake water-depth gradient: Effects of abiotic and biotic drivers, The Science of the Total Environment, 686: 1262-1271. https://doi.org/10.1016/J.SCITOTENV.2019.05.381