



# **UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO**

**POSGRADO EN CIENCIAS BIOLÓGICAS**

**INSTITUTO DE GEOLOGÍA**

**BIOLOGÍA EVOLUTIVA**

**(PROYECTO)**

**UN ENFOQUE DECONSTRUCTIVO PARA EVALUAR LOS PATRONES GEOGRÁFICOS DE  
RIQUEZA DE ANFIBIOS: ESCLARECIENDO LA IMPORTANCIA RELATIVA DE LOS FACTORES  
ECOLÓGICOS Y EVOLUTIVOS**

**TESIS POR ARTÍCULO CIENTÍFICO**

**A DECONSTRUCTIVE APPROACH REVEALS CONSISTENT EFFECTS OF ECOLOGICAL FACTORS  
DRIVING AMPHIBIAN RICHNESS ACROSS PHYLOGENETIC SCALES**

**QUE PARA OPTAR POR EL GRADO DE:**

**MAESTRO EN CIENCIAS BIOLÓGICAS**

**PRESENTA:**

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**RED DE BIOLOGÍA EVOLUTIVA, INECOL**

**CIUDAD UNIVERSITARIA, CD. MX. MARZO 2025**



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COORDINACIÓN GENERAL DE ESTUDIOS DE POSGRADO  
COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS  
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OFICIO: CGEP/CPCB/IGEL/0053/2025  
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Sin otro particular, me es grato enviarle un cordial saludo.

**ATENTAMENTE**  
**"POR MI RAZA HABLARÁ EL ESPÍRITU"**  
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## Agradecimientos institucionales

Al Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México, incluyendo a los docentes que participaron en mi formación académica a través de las materias impartidas en el posgrado y al personal administrativo que siempre me brindó su apoyo ante cualquier duda. A la Universidad Nacional Autónoma de México, por poner a mi disposición un sin fin de información y herramientas que me fueron de gran utilidad durante mi formación académica.

Al Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCyT), que ha pasado a ser la **Secretaría de Ciencia, Humanidades, Tecnología e Innovación** (SECIHTI), por el apoyo económico otorgado durante la realización de mi maestría (CVU/becario: 1194674/826247).

Este trabajo de tesis se realizó gracias al Programa UNAM-DGAPA-PAPIIT, en el marco del proyecto con clave IA206523: "Legados biogeográficos, evolutivos, y ecológicos para el entendimiento del impacto del cambio climático sobre ensambles de especies a escalas locales y regionales".

Al Dr. Julián Andrés Velasco Vinasco, Dra. Leticia Margarita Ochoa Ochoa y Dr. Crisóforo Fabricio Villalobos Camacho por su atención y tiempo al compartir parte de su conocimiento conmigo.

## **Agradecimientos a título personal**

A mis padres Rafael y Eva que siempre me han apoyado y creído en mis sueños a pesar de los tropiezos y contratiempos que he tenido.

A mi hermano, a Carlos y a mis primos con los que tuve contacto de manera más directa durante la duración de mi maestría, gracias por siempre escucharme cuando tenía preocupaciones y temores y no dudar en darme palabras que me reconfortaran.

A los miembros de la Colección Nacional de Anfibios y Reptiles del IBUNAM, gracias por permitirme ser un miembro más de ustedes e invitarme a eventos sociales y culturales.

A Andrés y Oswaldo, gracias por las pláticas y las salidas al campo.

A las demás amistades que hice durante la maestría, gracias por intercambiar experiencias conmigo y de manera especial a Gaby por invitarme a bailar.

A Julián por creer en mi proyecto, Lety por cuestionarme todo y Fabricio por haberme recibido en el INECOL dos semanas.

A los miembros del Jurado de tesis, Dra. Ella Vázquez, Dra. Gabriela Parra, Dr. Alejandro Voyer y Dr. Constantino González por sus valiosos comentarios que enriquecieron esta tesis.

## Contenido

|                                                                                                                                        |    |
|----------------------------------------------------------------------------------------------------------------------------------------|----|
| Resumen.....                                                                                                                           | 1  |
| Abstract .....                                                                                                                         | 2  |
| Introducción general .....                                                                                                             | 3  |
| A deconstructive approach reveals consistent effects of ecological factors driving amphibian richness across phylogenetic scales ..... | 6  |
| Abstract .....                                                                                                                         | 6  |
| 1. Introduction.....                                                                                                                   | 7  |
| 2. Methods .....                                                                                                                       | 10 |
| 2.1 Data compilation .....                                                                                                             | 10 |
| 2.2 Environmental and evolutionary factors .....                                                                                       | 10 |
| 2.3 Statistical analyses.....                                                                                                          | 11 |
| 3. Results .....                                                                                                                       | 12 |
| 3.1 Deconstruction of the geographical patterns of species richness .....                                                              | 12 |
| 3.2 Importance of ecological and evolutionary factors across phylogenetic scales.....                                                  | 14 |
| 4. Discussion.....                                                                                                                     | 16 |
| 5. Conclusions.....                                                                                                                    | 19 |
| References .....                                                                                                                       | 19 |
| Acknowledgments .....                                                                                                                  | 24 |
| Biosketch .....                                                                                                                        | 24 |
| Discusión general y conclusiones .....                                                                                                 | 25 |
| Referencias .....                                                                                                                      | 26 |

## Resumen

A pesar de la larga tradición de estudios sobre las causas de los patrones geográficos de riqueza de especies, no existe un consenso acerca de qué hipótesis pueden explicar la configuración de dichos patrones. Entre las causas de la falta de consenso están que la mayoría de los estudios consideran únicamente escalas filogenéticas amplias (por ejemplo, a nivel de clase), con el supuesto de que todas las especies y clados responden de la misma manera a los factores ecológicos y evolutivos. Sin embargo, se ha demostrado que los mecanismos que determinan los patrones de riqueza pueden variar según la historia evolutiva y/o la escala filogenética. En este estudio evaluamos la importancia de diferentes hipótesis ecológicas y evolutivas para explicar los patrones geográficos de riqueza de anfibios a través de un enfoque deconstructivo filogenético (familia, orden y clase). Para esto, utilizamos datos disponibles en bases de datos sobre distribuciones geográficas y en literatura científica sobre relaciones filogenéticas de anfibios, de variables climáticas actuales y pasadas, de complejidad topográfica y de altura del dosel. Utilizamos modelos de ecuaciones estructurales que incorporan autocorrelación espacial para analizar el efecto directo e indirecto de las variables estudiadas en los patrones de riqueza. Los resultados mostraron variación en la dirección del efecto de la mayoría de las variables en función de la escala filogenética e incluso entre grupos de anfibios de la misma escala. Sin embargo, encontramos un efecto positivo de la altura del dosel y un efecto negativo de la estacionalidad de la temperatura, los cuales se mantienen constantes en las diferentes escalas y en grupos de la misma escala. Asimismo, encontramos que las variables ecológicas influyen en la riqueza de manera directa más frecuentemente que de manera indirecta. Respecto a las variables evolutivas, sólo el efecto del tiempo evolutivo se mantuvo constante en al menos dos escalas (orden caudata y sus familias). Nuestro estudio destaca la importancia del espacio ecológico disponible, evaluado como altura del dosel y la estacionalidad de la temperatura, como promotores y limitantes de la riqueza de especies respectivamente. Ello tiene sentido considerando que la mayoría de los anfibios son especialistas en cuanto a hábitat y con distribuciones restringidas. Por otra parte, las variables ecológicas también pueden sugerir como otras variables evolutivas que no se evaluaron pueden asociarse a la configuración de los patrones observados. Por ejemplo, cambios extremos de temperatura y fuerte estacionalidad podrían limitar la adaptación, produciendo extinción y limitando la dispersión/colonización de las especies, dada la limitada amplitud de nicho de los anfibios en general.

## Abstract

Despite a long tradition of studies on the causes of geographic patterns of species richness, there is no consensus about which hypotheses can explain the configuration of such patterns. Among the reasons for the lack of consensus are that most studies consider only broad phylogenetic scales (for example, at the class level), with the assumption that all species and clades respond in the same way to ecological and evolutionary factors. However, it has been shown that the mechanisms that determine richness patterns can vary according to evolutionary history and/or phylogenetic scale. In this study we evaluate the importance of different ecological and evolutionary hypotheses to explain geographic patterns of amphibian richness through a deconstructive phylogenetic approach (family, order and class). To do so, we use data available in databases on geographic distributions and in scientific literature on phylogenetic relationships of amphibians, current and past climatic variables, topographic complexity and canopy height. We used structural equation models incorporating spatial autocorrelation to analyze the direct and indirect effect of the variables studied on richness patterns. The results showed variation in the direction of the effect of most variables depending on the phylogenetic scale and even between groups of amphibians at the same scale. However, we found a positive effect of canopy height and a negative effect of temperature seasonality, which remained constant at different scales and in groups at the same scale. Likewise, we found that ecological variables influence richness directly more frequently than indirectly. Regarding evolutionary variables, only the effect of evolutionary time remained constant in at least two scales (order Caudata and its families). Our study highlights the importance of available ecological space, evaluated as canopy height and temperature seasonality, as promoters and limiters of species richness respectively. This makes sense considering that most amphibians are habitat specialists with restricted distributions. On the other hand, ecological factors may also suggest how other, unassessed evolutionary mechanisms may be involved in shaping patterns. For example, rapid changes in temperature or strong seasonality may limit species adaptation, causing extinction and limiting dispersal/colonization given the narrow niche breadth of amphibians in general.

## Introducción general

Una larga tradición de estudios en biogeografía y ecología ha intentado comprender el origen y el mantenimiento de los gradientes geográficos de gran escala en la diversidad, específicamente el gradiente latitudinal de diversidad (GLD) (Saupe, 2023). Estos estudios han propuesto diversas hipótesis para explicar el GLD, relacionándolo con la variación geográfica de al menos un factor ecológico o evolutivo (Wiens et al., 2006). A pesar de esto, no existe consenso sobre qué hipótesis explican mejor el GLD entre taxones (Buckley et al., 2010). Los estudios pioneros sobre las causas de los gradientes de diversidad geográfica solo se centraron en el papel de los factores ecológicos (p. ej., Wright, 1983; Currie, 1991; O'Brien et al., 2000). Posteriormente, con el avance de los métodos filogenéticos moleculares, algunos estudios evaluaron únicamente el papel de los factores evolutivos en la configuración de estos patrones (p. ej., Weir & Schluter, 2007; Jetz et al., 2012; Rolland et al., 2014), y otros incluso analizaron la relación conjunta entre los factores ecológicos y evolutivos en la configuración de dichos gradientes (p. ej., Buckley et al., 2010; Pyron & Wiens, 2013; García-Andrade et al., 2023).

De acuerdo con lo anterior, las principales hipótesis propuestas para explicar la riqueza de especies se pueden dividir en dos grandes grupos: ecológicas y evolutivas (Buckley et al., 2010). El primer grupo incluye varias hipótesis contemporáneas e históricas recientes que plantean cómo diferentes ejes ambientales pueden explicar por qué hay tantas especies en algunos lugares (Willig et al., 2003). Por ejemplo, la hipótesis de productividad plantea que ambientes con mayor productividad permiten la coexistencia de más individuos y, por lo tanto, un mayor número de especies (Hawkins et al., 2003). La hipótesis de estacionalidad plantea que la estacionalidad climática limita la diversidad ya que las especies necesitan desarrollar amplias tolerancias ambientales que impiden la especialización y pueden promover la competencia debido a los amplios rangos de distribución (Klopfer, 1959; Stevens, 1989). La hipótesis de heterogeneidad ambiental plantea que los sitios con mayor complejidad física tendrán mayor espacio ambiental (es decir, espacio ecológico) disponible, lo que permitirá la coexistencia de más especies (Currie, 1991; Hawkins et al., 2003). La hipótesis de estabilidad climática histórica reciente establece que los lugares donde el clima ha cambiado poco desde el pasado (por ejemplo, desde el Pleistoceno) tendrán tasas de extinción más bajas y acumularán más especies, promoviendo la especialización de nichos y, por lo tanto, la diversificación de especies (Araújo et al., 2008).

El segundo grupo de hipótesis enfatiza cómo los procesos de tiempo profundo relacionados con la dinámica de diversificación de especies y eventos biogeográficos históricos pueden explicar los gradientes de diversidad geográfica contemporáneos (Mittelbach et al., 2007). Al menos dos hipótesis han sido evaluadas extensivamente en la literatura: tiempo evolutivo y tasa de diversificación. La hipótesis del tiempo evolutivo establece que los lugares donde los linajes han estado presentes por mucho tiempo habrán tenido más oportunidades de diversificarse y acumular nuevas especies (Currie, 1991; Wiens et al., 2007). La hipótesis de la tasa de diversificación establece que la riqueza de especies será mayor en aquellos sitios con tasas de diversificación más altas, generando así más especies (es decir, especiación) que las pérdidas por extinción (Mittelbach et al., 2007).

Aunque se ha demostrado ampliamente que los patrones de riqueza y su relación con los factores que los impulsan pueden depender de la escala espacial y temporal en la que se analizan (Graham et al., 2018), el papel de la escala filogenética no se entiende bien. Esto se debe a que, por lo general, dichos estudios han realizado sus análisis a grandes escalas filogenéticas (por ejemplo, una clase taxonómica completa de organismos como plantas vasculares, mamíferos o aves), y solo recientemente se ha implementado un enfoque deconstructivo para desentrañar el papel relativo de los diferentes factores que configuran la diversidad de especies en varias escalas filogenéticas (por ejemplo, Buckley et al., 2010; García-Andrade et al., 2023). Analizar los patrones de riqueza de especies y sus impulsores exclusivamente a una escala filogenética amplia supone que todas las especies y clados exhiben una respuesta similar a los factores contemporáneos e históricos, agrupando los roles de los mecanismos ecológicos y evolutivos en un resultado general (Marquet et al., 2004). Sin embargo, los mecanismos que determinan los patrones de riqueza pueden variar según la escala filogenética y/o el grupo taxonómico analizado (Graham et al., 2018). En consecuencia, un tratamiento más riguroso a través de las escalas filogenéticas podría producir una comprensión más profunda de los procesos que dan lugar a los patrones de riqueza geográfica.

Estudios previos han aportado evidencia de que los factores ecológicos que mejor explican la variación geográfica de la riqueza de especies de anfibios a nivel de clase son la productividad (p. ej., Buckley y Jetz, 2007; Gouveia et al., 2012) o la altura del dosel (Barreto et al., 2021). Por el contrario, otros estudios que evalúan factores evolutivos han encontrado que el tiempo evolutivo (Marin y Hedges, 2016; Marin et al., 2018; García-Rodríguez et al., 2020) o la variación en las tasas de diversificación (Pyron y Wiens, 2013) son los impulsores más importantes de la riqueza de especies. Además, en los casos en los que se evaluó el efecto indirecto de los factores ecológicos sobre la riqueza a través de los factores evolutivos, se encontró que era significativo (Pyron y Wiens, 2013; Marin et al., 2018; García-Rodríguez et al., 2020). Adicionalmente, algunos estudios han examinado los efectos de dichos factores en clados pertenecientes a escalas filogenéticas inferiores (es decir, familias u órdenes) y han descubierto que el tiempo evolutivo predice en gran medida la riqueza de especies en Hylidae (Wiens et al., 2006), Plethodontidae (Wiens et al., 2007) y Caudata (Cerezer et al., 2022). Sin embargo, aún existen grupos en los que no se han analizado las relaciones de los factores ecológicos y evolutivos con sus patrones de riqueza. Además, hasta donde sabemos, ningún estudio ha analizado conjuntamente el papel relativo de los factores ecológicos y evolutivos en la configuración de los patrones de riqueza de anfibios utilizando un enfoque filogenético deconstructivo.

En este trabajo evaluamos la contribución directa e indirecta de los factores ecológicos y evolutivos que configuran el patrón geográfico de riqueza de especies según varias hipótesis y en diferentes niveles de escala filogenética dentro de Amphibia. Específicamente, probamos si las relaciones ambientales/históricas de riqueza de especies se mantienen en la gran radiación de anfibios a nivel global y en los principales subclados inclusivos (órdenes y familias). Este enfoque nos permitió identificar en qué escalas filogenéticas (o grupos de la misma escala) la interacción de ciertos factores ecológicos y evolutivos genera y mantiene el patrón general de riqueza de especies o patrones diferentes, además discutimos las posibles causas.

A deconstructive approach reveals consistent effects of  
ecological factors driving amphibian richness across  
phylogenetic scales

Sometido a la revista *Global Ecology and Biogeography*

# **A deconstructive approach reveals consistent effects of ecological factors driving amphibian richness across phylogenetic scales**

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**Short running title:** Temperature seasonality and canopy height drive amphibian richness

## **Abstract**

**Aim:** Despite decades of research on the latitudinal diversity gradient (LDG), a comprehensive understanding of its ecological and evolutionary causes and their interplay at different phylogenetic scales remains elusive. Here, we implement a deconstructive macroecological approach to investigate how various ecological and evolutionary factors jointly influence the observed latitudinal diversity gradient in amphibians across different Linnean ranks (i.e., orders and families).

**Location:** Globally

**Time period:** Deep past and present

**Major taxa:** Amphibia

**Methods:** We used available data on amphibian geographical distributions and phylogenetic relationships. We compiled information about speciation rates, evolutionary time, productivity, climate seasonality, past climate stability, topographic complexity and canopy height to evaluate how these factors and their interplay have shaped the current geographical species richness patterns across the Amphibian class, its orders and families. We used structural equation models incorporating spatial autocorrelation to analyze the direct and indirect influences of these factors on the LDGs.

**Results:** Our findings confirmed that amphibians follow the typical LDG at the class level. However, different patterns can emerge at lower phylogenetic levels (e.g., inverse LDG in Salamandridae). Ecological factors generally contribute to shaping spatial richness, highlighting the generally constant effects of canopy height (positive) and temperature seasonality (negative). However, evolutionary factors rarely contribute to the richness patterns, except evolutionary time, which maintain a constant effect in salamanders (positive). Ecological factors rarely influence richness indirectly.

**Main conclusions:** Our study provides evidence that temperature seasonality and canopy height

play a substantial role in determining the LDG observed in amphibians. Demonstrating for the first time a stationary environmental-richness relationship across phylogenetic scales in this group. These findings and the constant effect of evolutionary time found in salamanders support the need to simultaneously assess which ecological and evolutionary factors, as well as their interactions, determine LDG and whether its importance is maintained across phylogenetic scales.

**Keywords:** Anura, Caudata, diversity gradient, environmental stress, evolutionary time, Gymnophiona, macroecology, speciation rate.

## 1. Introduction

A long tradition of studies in biogeography and ecology has attempted to understand the origin and maintenance of large-scale geographical gradients in diversity, specifically the latitudinal diversity gradient (LDG) (Saupe, 2023). These studies have proposed many hypotheses to explain the LDG by relating them to the geographical variation of at least one ecological or evolutionary factor (Wiens et al., 2006). Despite this, no consensus exists on which hypotheses best explain the LDG across taxa (Buckley et al., 2010). Pioneering studies on the causes of geographical diversity gradients only focused on the role of ecological factors (e.g., Wright, 1983; Currie, 1991; O'Brien et al., 2000). Subsequently, with the advance of molecular phylogenetic methods, some studies evaluated only the role of evolutionary factors shaping these patterns (e.g., Weir & Schluter, 2007; Jetz et al., 2012; Rolland et al., 2014), and others even analyzed the joint relationship between ecological and evolutionary factors in shaping latitudinal diversity gradients (e.g., Buckley et al., 2010; Pyron & Wiens, 2013; García-Andrade et al., 2023).

Accordingly, the main hypotheses proposed to explain such diversity patterns, namely species richness, can be divided into two major groups: ecological and evolutionary (Buckley et al., 2010). The first group includes several contemporary and recent historical hypotheses that state how different environmental axes can explain why there are so many species in some places (Willig et al., 2003; see table 1 for some examples). The second group of hypotheses emphasizes how deep-time processes related to species diversification dynamics and historical biogeographic events can explain contemporary geographical diversity gradients (Mittelbach et al., 2007; see table 1 for some examples). Despite this, to recognize which hypothesis (or group of them) and underlying mechanism is most important in determining species richness patterns, it is necessary to evaluate multiple hypotheses and their relationships simultaneously. This is because, on the one hand, regional species richness can be modified by evolutionary factors that generate (speciation), eliminate (extinction) and/or allow species to accumulate (dispersal). On the other hand, ecological factors can modulate both the speciation-extinction balance and the dispersion balance (thus facilitating colonization) according to the region's available ecological space and lineage occurrence (Saupe, 2023; García-Andrade et al., 2023).

**Table 1.** Main hypotheses posed in the literature to explain geographical diversity gradients. In the second column, the letter D indicates direct mechanisms, while the letter I indicates indirect mechanisms. The third column lists the variable used to test each hypothesis in this study. The fourth column contains examples of studies evaluating the relative support for each hypothesis.

| Hypothesis | Mechanism | Variable used | Studies |
|------------|-----------|---------------|---------|
|------------|-----------|---------------|---------|

|                              |                                                                                                                                                               |                                                         |                                                                                                          |
|------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------|----------------------------------------------------------------------------------------------------------|
| Productivity                 | D: Sites with greater productivity will support more individuals, determining the maximum number of viable populations and species.                           | Actual evapotranspiration.                              | Birds globally (Hawkins et al., 2003), amphibians globally (Buckley & Jetz, 2007; Gouveia et al., 2012). |
| Seasonality                  | D: Developing broad environmental tolerances prevents specialization and promotes exclusion due to competitiveness.                                           | Temperature and precipitation seasonality.              | Amphibians globally (Gouveia et al., 2012), vascular plants globally (Cai et al., 2022)                  |
| Historical climate stability | D: Lower extinction rates in stable sites / I: high speciation rates in stable sites / I: stable sites offer more time to accumulate species.                 | Velocity of climate change.                             | Montane amphibians (García-Rodríguez et al., 2020), vascular plants globally (Cai et al., 2022)          |
| Environmental heterogeneity  | D: It offers greater ecological/climate space to maintain a higher diversity of species / I: Due to geographical barriers, it promotes allopatric speciation. | Topographic heterogeneity.                              | Vascular plants globally (Cai et al., 2022), Australasian and Neotropical Parrots (Davies et al., 2007). |
|                              | D: It offers greater ecological space available to house species.                                                                                             | Canopy height.                                          | Parrots globally (Davies et al., 2007).                                                                  |
| Diversification rates        | D: Faster speciation rates allow for more rapid species accumulation than sites with slower speciation rates.                                                 | Mean of tip-rate speciation for species assemblage.     | Foraminifera globally (Allen & Gillooly, 2006), mammals globally (Rolland et al., 2014),                 |
| Evolutionary time            | D: Greater time for speciation and accumulation by dispersal.                                                                                                 | Mean of maximum branch lengths for species assemblages. | Montane amphibians (García-Rodríguez et al., 2020), freshwater Actinopterygii globally (García-          |

|  |  |  |                        |
|--|--|--|------------------------|
|  |  |  | Andrade et al., 2023). |
|--|--|--|------------------------|

Although it has been widely shown that richness patterns and their relationship to the factors driving them can depend on the spatial and temporal scale at which they are analyzed (Graham et al., 2018), the role of phylogenetic scale is not well understood. This is because typically such studies have performed their analyses at large phylogenetic scales (e.g., an entire taxonomic class of organisms such as vascular plants, mammals, or birds), and only recently has a deconstructive approach been implemented to disentangle the relative role of different factors shaping species diversity at various phylogenetic scales (e.g., Buckley et al., 2010; García-Andrade et al., 2023). Analyzing patterns of species richness and their drivers exclusively at broad phylogenetic scales assumes that all species and clades exhibit a similar response to contemporary and historical factors, pooling the roles of ecological and evolutionary mechanisms into one general result (Marquet et al., 2004). However, the mechanisms determining richness patterns can vary depending on the level of the phylogenetic scales and/or taxonomic group analyzed (Graham et al., 2018). Accordingly, a more rigorous treatment across phylogenetic scales could produce a deeper understanding of the processes that give rise to geographical richness patterns.

Amphibians are ectothermic vertebrates originating from the Permian period (about 290 Ma). They are characterized by having water-permeable skin that functions as an essential respiratory organ, so it must always be moist to allow gas exchange and they need to maintain a balance between heat gain and water loss (Vitt & Caldwell, 2014). Because of this, amphibians are very sensitive to environmental change (Wake & Vredenburg, 2008). Amphibians are currently represented by more than 8,700 species included in three orders: Anura (> 7,690 spp.), Caudata (> 820 spp.), and Gymnophiona (> 220 spp.) (Frost, 2024). Previous studies have provided evidence that the ecological factors that best explain the variation in species richness across geography are productivity (e.g., Buckley & Jetz, 2007; Gouveia et al., 2012) or canopy height (Barreto et al., 2021). By contrast, other studies assessing evolutionary factors have found that evolutionary time (Marin & Hedges, 2016; Marin et al., 2018; García Rodríguez et al., 2020) or variation in diversification rates (Pyron & Wiens, 2013) are the most important drivers of species richness. Furthermore, in cases where the indirect effect of ecological factors through evolutionary factors was analyzed, it was found to be significant (Pyron & Wiens, 2013; Marin et al., 2018; García Rodríguez et al., 2020). Additionally, few studies have analyzed the causes of richness patterns at lower phylogenetic scales (i.e., families or orders), and found that evolutionary time greatly predicts species richness in Hylidae (Wiens et al., 2006), Plethodontidae (Wiens et al., 2007), and Caudata (Cerezer et al., 2022). However, to our knowledge, no study has jointly analyzed the relative role of ecological and evolutionary factors across several phylogenetic scales in amphibians using a deconstructive macroecological approach.

Here, we evaluated the direct and indirect contribution of ecological and evolutionary factors shaping the geographical pattern of species richness according to several hypotheses and across different phylogenetic scales within Amphibia. Specifically, we tested whether the environmental/historical species richness relationships are maintained in the large radiation of amphibians globally and across the main inclusive subclades (orders and families). This approach

allowed us to identify at which phylogenetic scales the interaction of certain ecological and evolutionary factors generates and maintains the general pattern of species richness or differs from it.

## **2. Methods**

### **2.1 Data compilation**

Distributional data for amphibian species in the form of range maps (polygons) were obtained from the IUCN (IUCN, 2023). Using these maps, we generated richness maps for the entire class, each order (Anura, Caudata, and Gymnophiona), and the two most diverse families within each order (Hylidae and Strabomantidae for Anura; Plethodontidae and Salamandridae for Caudata; and Caeciliidae and Ichthyophiidae for Gymnophiona). We did this by superimposing a 100 km equal-area grid (Mollweide projection) onto the species' range maps and constructing a presence-absence matrix using the *lets.presab* function from the *letsR* v. 4.0 R package (Villela & Villalobos, 2005). Phylogenetic relationships among amphibian species were obtained from the most complete and time-calibrated phylogeny of existing amphibians (Jetz & Pyron, 2018), including 100 phylogenetic trees of the pseudo posterior distribution of the extended phylogeny. Due to the taxonomic variation that may be present between different data sources, names in the phylogenies were standardized based on IUCN names, and species that were not present in both data sources were removed so that the species analyzed included only those that had both phylogenetic information and information on their geographic distribution. To do this, we corroborated the identity of the species from both data sources based on Amphibiaweb (2024) and standardized the names in the phylogenies with the names included in the IUCN polygons (IUCN, 2023). We then eliminated those species present in the phylogenies but lacking a distribution polygon in the IUCN database using the *drop.tip* function of the *ape* v. 5.7-1 R package (Paradis & Schielp, 2019); finally, we excluded the polygons of the species that were not present in the phylogenies.

### **2.2 Environmental and evolutionary factors**

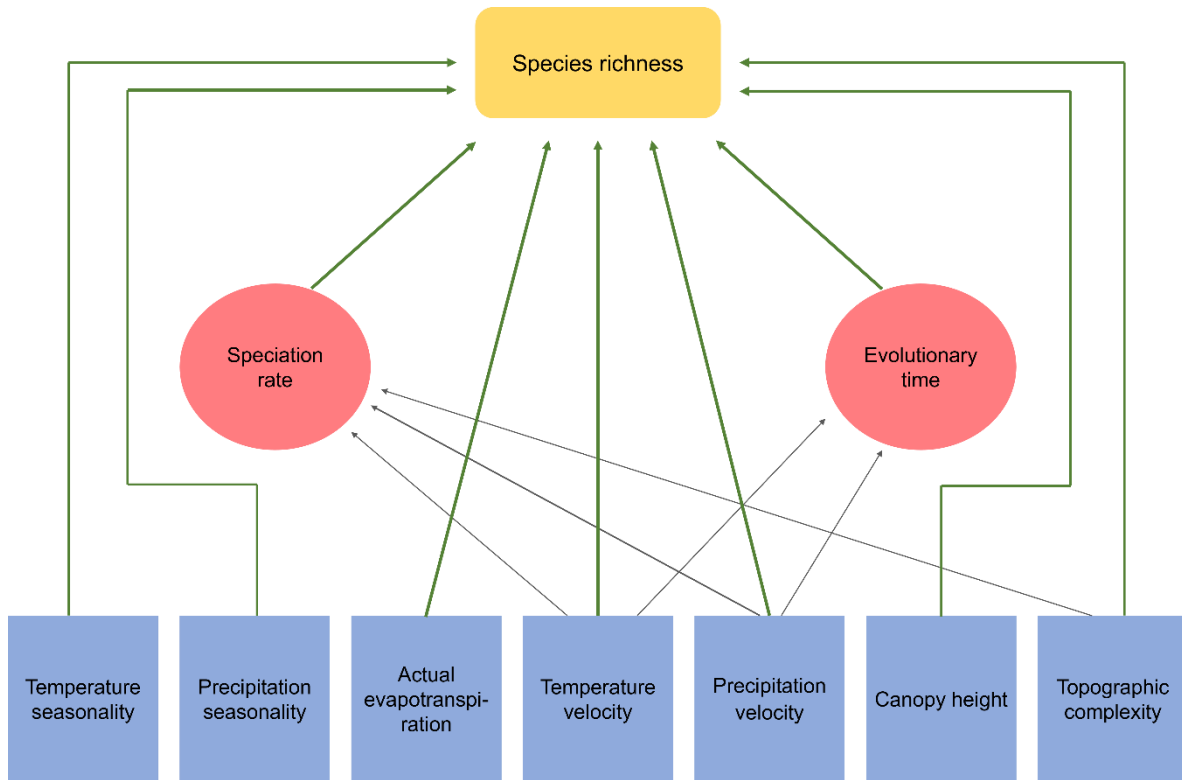
To evaluate the effects of the various factors potentially driving the geographical variation in amphibian species richness, we evaluated six ecological hypotheses that have been widely proposed to explain richness patterns in multiple groups, both animals and plants. Importantly, these factors may act directly or indirectly (Table 1). To test the environmental productivity hypothesis, the actual evapotranspiration rate (AET) was used, which has a high correlation with primary productivity (Rosenzweig, 1968). The seasonality hypothesis was evaluated using temperature seasonality (BIO4; EstTemp) and precipitation seasonality (BIO15; EstPrec) from WorldClim v.2 at a resolution of 10 minutes (Fick & Hijams, 2017). To analyze the importance of the environmental heterogeneity hypothesis, topographic complexity (Tcomp) was taken from the topographic heterogeneity index (TH8: [www.ipez.es/Modets tr/](http://www.ipez.es/Modets%20tr/)), which describes how different the topography of a cell is in relation to its neighboring cells, considering elevation, slope, and aspect of the slope (Pelayo-Villamil et al., 2015). As an approximation of the available vertical ecological space, vegetation heterogeneity (Treeh) was evaluated by using the global map of forest canopy height (Potapov et al., 2020). Historical climate stability was estimated as the velocity of climate change, calculated by dividing the rate of climate change over time since the Last Glacial Maximum by the local rate of climate change across space (Sandel et al., 2011). We calculated the velocity of climate change for annual mean temperature (VelTemp) and total annual precipitation

(VelPrec) using past climate information available in PaleoClim (Brown et al., 2018). The average values of these factors were obtained for each grid cell using Mollweide projection to match the resolution of our estimates of species richness.

As part of the evolutionary hypotheses, a proxy of the mean speciation rate was estimated with the DR metric (lineage speciation rate at the species level; Jetz et al., 2012) using custom functions from Velasco and Pinto-Ledezma (2022). To estimate the time that the oldest taxon has been present in each cell, the maximum branch length (MBL) was calculated based on each grid-cell assemblage, using custom functions from Velasco and Pinto-Ledezma (2022). This metric was used because previous studies have found that it is a good proxy of evolutionary time, showing a positive and significant relationship with age of first colonization (García-Andrade et al., 2023) and without presenting a relationship between the age and range size of amphibian species (García-Rodríguez et al., 2020). For each grid cell, we calculated the mean (mDR) and the mean MBL across the 100 phylogenetic trees of the pseudo posterior distribution.

### 2.3 Statistical analyses

A piecewise structural equation modeling approach (pSEM) was implemented to evaluate the effects of environmental and evolutionary mechanisms and their interactions on species richness patterns (García-Andrade et al., 2023). We proposed a theoretical model describing how species richness is linked directly and indirectly to each factor while considering their interaction (Fig. 1). The pSEM consists of different paths, each one considering a single response factor (richness, evolutionary time, or speciation rate) and the independent factors that directly influence them. In our case, we established three routes: the first corresponding to those factors that influence the speciation rate, the second to those factors that influence evolutionary time, and the third to the factors that influence species richness. Prior to running the pSEM, values of the predictor factors were standardized to a mean of zero and standard deviation of one to allow for direct comparisons of the model coefficients. Subsequently, a model selection procedure was performed for each path, testing differences in distances and spatial weight matrices under a spatial autoregressive (SAR) model to find the best combination of parameters that eliminated spatial autocorrelation in residuals. SAR models were run using the *spdep* v. 1.2-8 and *spatialreg* v.1.2-9 R packages (Bivand et al., 2013). Then, the theoretical model was fitted using the *psem* function of the *piecewiseSEM* v. 2.3.0 R package (Lefcheck, 2016), and based on the results of d-separation tests for local estimates (each path), which evaluate whether important (causally dependent) relationships are missing in the model; If missing relationships without theoretical foundation existed, they were added as correlated errors. Finally, the model was run again with the same function. In the final model, obtaining a Fisher's C statistic value > 0.05 implies a good fit and no missing relationships. The total effects of the factors were calculated as the sum of the direct and indirect effects. This procedure was repeated independently for the entire class, all three orders, and the selected families.

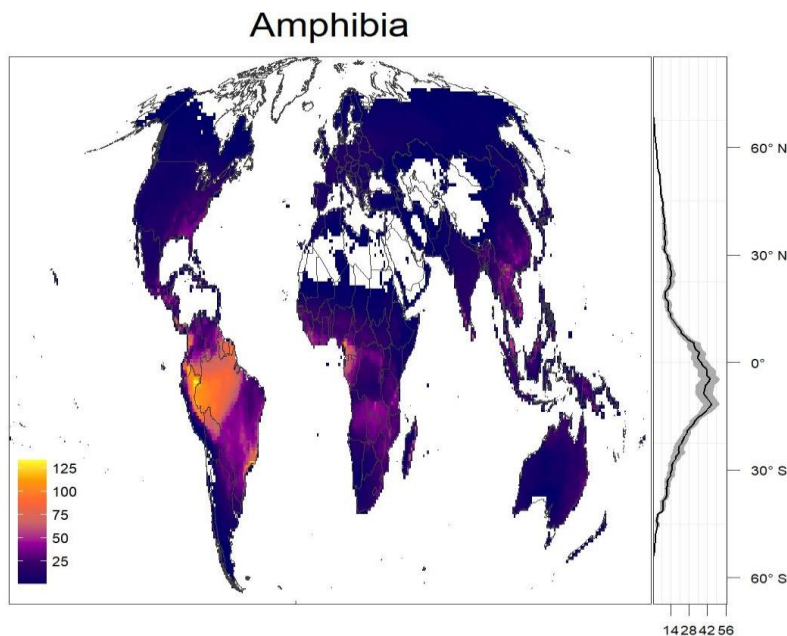


**Figure 1.** Theoretical model proposed to explain the origin and maintenance of the geographical pattern of species richness across the entire class of Amphibians and different phylogenetic levels (orders and families) with a set of relevant ecological and evolutionary factors. Gray arrows indicate indirect effects on species richness, while green arrows indicate direct effects. Blue boxes indicate ecological factors, and red circles indicate evolutionary factors.

### 3. Results

#### 3.1 Deconstruction of the geographical patterns of species richness

The geographical species richness patterns for Amphibia and Anura were very similar as both groups are widely distributed globally and have two areas of peak richness, one in South America and the other on the west coast of Africa (Figs. 2, 3A). Conversely, we found striking differences between the patterns of the Amphibia class and those of the orders Caudata and Gymnophiona. Caudata, with a very restricted distribution in Africa and southern Asia and being completely absent from Australia, exhibits two areas of peaks of richness, one in the eastern United States and the other in Costa Rica (Fig. 3D). By contrast, Gymnophiona is practically restricted to tropical areas (although it also occurs in a small part of the southern temperate region) and shows its greatest richness in northern South America (Fig. 3G). In addition, the Amphibia class as a whole, as well as the Anura order exhibit the classic latitudinal diversity gradient (LDG), with a peak of species richness at or near the equator (Figs. 2, 3A). By contrast, Caudata and Gymnophiona orders exhibited two diversity peaks (a bimodal pattern). Caudata presents one peak in the tropical region and another in the northern temperate region (Fig. 3D), while Gymnophiona presents one in the tropical zone and another in the southern temperate region, just before 30° S (Fig. 3G).

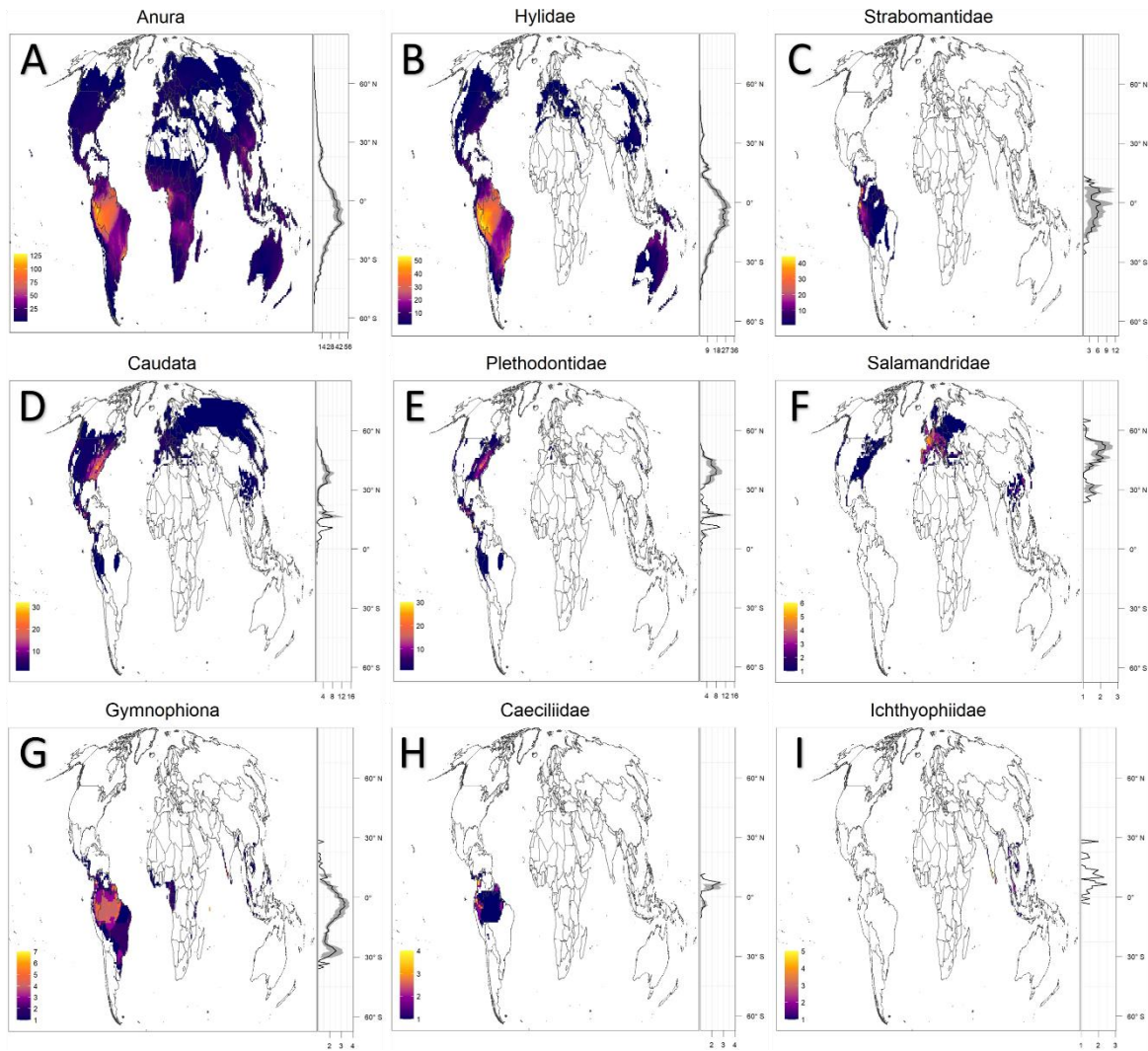


**Figure 2.** Species richness map of the Amphibia class with its latitudinal pattern.

Regarding the families within Anura, Hylidae exhibited a more similar pattern to Anura, and is distributed in both tropical and temperate regions (Fig. 3B). By contrast, Strabomantidae is restricted to the Neotropical region (Fig. 3C). Both families presented their highest richness in the Neotropical region, like Anura, but not in Africa, and showed a typical LDG (Figs. 3A–C).

Considering the Salamandridae and Plethodontidae families within Caudata, we found differences in the geographical patterns of species richness (Figs. 3E–F). Plethodontidae is mainly concentrated in the American continent (Fig. 3E), while Salamandridae is broadly distributed in Europe (Fig. 3F). The Plethodontidae family presents two areas of highest richness, both of which are shared with Caudata (Figs. 3D–E). Salamandridae’s highest richness is in Europe (Fig. 3F), not coinciding with any of the areas of the other groups (Figs. 3D–F). Caudata and Plethodontidae exhibit a similar bimodal pattern across the latitudinal gradient, with one peak in the tropical region above the equator and the other in the northern temperate region (Figs. 3D–E), while Salamandridae exhibit an inverse LDG, with one peak in the northern temperate region (Fig. 3F).

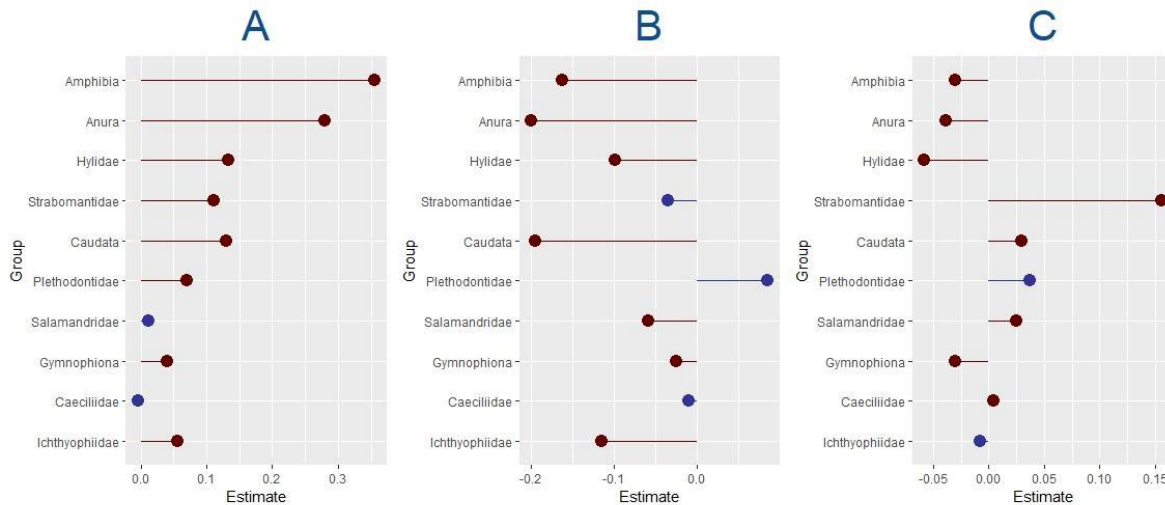
For Gymnophiona’s families, we found that Caeciliidae and Ichthyophiidae do not share overlapping distribution areas (Figs. 3H–I). While Caeciliidae is restricted to Central and South America (Fig. 3H), Ichthyophiidae is distributed exclusively in Southeast Asia (Fig. 3I). Like Gymnophiona, the area with the highest species richness of Caeciliidae is in northern South America (Figs. 3G–H), while for Ichthyophiidae it is located in southwest India (Fig. 3I). Both families showed the highest species richness at or near the equator, coinciding with Gymnophiona; however, unlike the entire order that presents a bimodal pattern (Fig. 3G), both families present the typical LDG (Figs. 3H–I).



**Figure 3.** Species richness maps for orders and families analyzed with their latitudinal patterns: A) Anura, B) Hylidae, C) Strabomantidae, D) Caudata, E) Plethodontidae, F) Salamandridae, G) Gymnophiona, H) Caeciliidae, I) Ichthyophiidae.

### 3.2 Importance of ecological and evolutionary factors across phylogenetic scales

The factor that most frequently influenced species richness across phylogenetic scales and among groups of the same level was canopy height, with a significant positive effect in eight groups (Fig. 4A). Meanwhile, the factor that most frequently influenced richness with a significant negative effect was seasonality of temperature (in seven groups; Fig. 4B). Another factor that frequently and significantly affected species richness but whose direction varied between groups was topographic complexity (negative in four groups, and positive in four; Fig 4C). The factor that least frequently influenced species richness with a positive significant effect was speciation rate (in two groups; Figs. 5A, 5I), while the factor that least frequently influenced species richness with a negative significant effect was velocity of temperature change (in three groups; Figs. 5D, 5G, 5I).

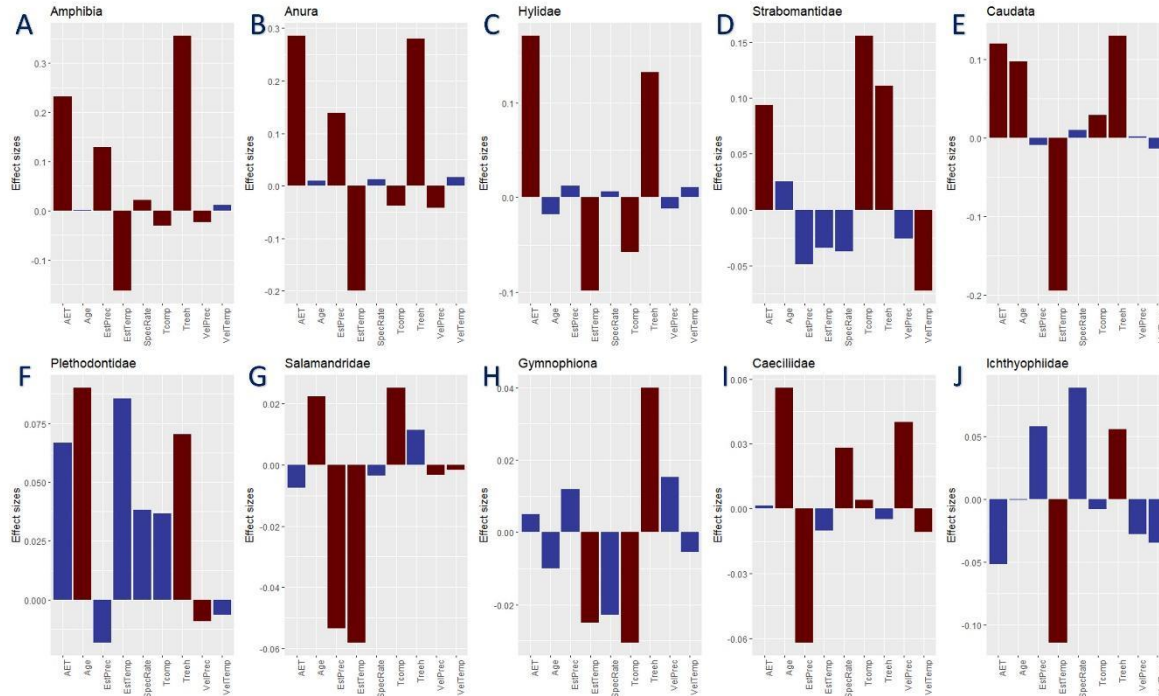


**Figure 4.** The most frequent factors significantly affecting species richness of the studied groups were A) canopy height, B) temperature seasonality, and C) topographic complexity. Bars and circles in dark red indicate significant effects, bars and circles in dark blue indicate non-significant effects.

The positive, significant effect of canopy height and the negative, significant effect of temperature seasonality on species richness was shared between the entire class and all three orders (Figs. 4A, B). Concerning Anura and its representative families, they only shared the positive, significant effects of canopy height (Fig. 4A) and actual evapotranspiration (Figs. 5B, 5C, 5D). On the other hand, Caudata and its representative families only shared the positive, significant effect of evolutionary time (Figs. 5E, 5F, 5G). Finally, no effects were found to be significant with the same direction between Gymnophiona and its representative families (Figs. 5H, 5I, 5J).

Only in a few groups did we find a significant, indirect effect of ecological factors on species richness. Topographic complexity positively affected species richness of amphibians at class level and in Caeciliidae through speciation rates. Velocity of precipitation change negatively affected evolutionary time in Plethodontidae and Salamandridae, however evolutionary time positively affected species richness. Finally, velocity of temperature change negatively affected evolutionary time in Caeciliidae and Salamandridae, however evolutionary time positively affected species richness.

In all groups, one of the ecological factors analyzed was found to be the best predictor of species richness, except in the Plethodontidae family, where the best predictor was evolutionary time (Fig. 5F). Of the ecological factors, only velocity of precipitation change and velocity of temperature change were not found to be the best predictors of species richness in at least one group analyzed, and temperature seasonality was the best predictor of richness with highest frequency, in three groups (Figs. 5E, 5G, 5J).



**Figure 5.** Total effect size of each of the evolutionary and ecological factors considered for A) Amphibia, B) Anura, C) Hylidae, D) Strabomantidae, E) Caudata, F) Plethodontidae, G) Salamandridae, H) the Gymnophiona, I) Caeciliidae and J) Ichthyophiidae. Bars in dark red indicate significant effects, while bars in dark blue indicate non-significant effects.

#### 4. Discussion

Our study suggests the importance of canopy height and temperature seasonality as the main ecological determinants of species richness (positive and negative respectively) in the class Amphibia. Furthermore, we found that their effects generally remain constant across the phylogenetic scales (from class to orders to families) and among groups of the same taxonomic hierarchy. The effects of evolutionary factors were more variable, as neither evolutionary time nor speciation rates were found to be important in determining species richness in some groups. However, this was not the case for salamanders, where the positive effect of evolutionary time remains constant throughout the order and its families. An indirect effect of ecological factors on richness was found only in a few groups, highlighting the positive effect of topographic complexity through speciation rates.

Due to the physiological characteristics of amphibians (humidity dependence and ectothermy) and the fact that amphibian species are generally climate and habitat specialists (e.g., Elias, 1984), it is not surprising that ecological factors were found to be important in shaping patterns of amphibian richness across the phylogenetic scales and in several groups of the same phylogenetic hierarchy. Considering the fact that these factors can modulate the processes of speciation, extinction, and dispersal, isn't surprising that some studies have suggested that the extinction rate of amphibians could be very high in the face of climate change caused by global warming (Wake & Vredenburg 2008). The lack of importance we found for evolutionary factors in shaping richness patterns in

frogs and most caecilians does not mean that evolutionary factors are not important, but rather that some other factors, such as extinction and dispersal rates, which we did not use, may be contributing to explaining the observed patterns. For example, Pyron and Wiens (2013) found that speciation rates determine species richness for the entire class, but that extinction and dispersal rates also contribute to this pattern.

Our study confirms what has been previously reported for the entire Amphibia class, that canopy height is the most important ecological factor in shaping richness patterns, and that its effect is positive (Roll et al., 2015), with regions harboring taller forest and thus higher structural complexity harboring higher species richness. More importantly, we also report herein that this factor has a similar effect across the phylogenetic scales (order and families) and across different groups of the same hierarchical level, which had not been previously evaluated or reported. Canopy height is a proxy for the available ecological space, so the higher the canopy height, the larger the ecological space exists to facilitate both coexistence and ecological diversification mechanisms (Oliveria & Scheffers, 2019). This impact is particularly evident in those clades that have developed adaptations for arboreal life, such as Hylidae, Plethodontidae, and Strabomantidae. As an example, Moen and Wiens (2017) found that, in general, anuran families with higher proportions of arboreal species have higher net diversification rates compared to less arboreal groups.

In the cases of groups that do not contain arboreal species but still present a positive relationship between species richness and canopy height (Gymnophiona and Ichthyophiidae), this may be due to the fact that as canopy height increases, the temperature inside the forest decreases, capping the maximum temperature (Jucker et al., 2018). Additionally, canopy height can be correlated with greater canopy cover, mainly in tropical regions (Kay et al., 2021). In turn, denser cover is associated with greater buffering of extreme climatic conditions in the forest (e.g., maximum temperature and minimum relative humidity), as well as lower soil temperature (Hardwick et al., 2015), which may be essential for the survival of caecilians due to their physiological characteristics and fossorial habits (Vitt & Caldwell, 2014). In fact, canopy cover has been found to be positively correlated with soil macrofauna biomass (Martius et al., 2004).

The relationship between temperature seasonality and species richness in amphibians has rarely been evaluated; however, at the class-wide level, Gouveia et al. (2012) reported that it is one of the main predictors of richness. In this study, we confirm this result at the class level, while additionally reporting that the negative effect of this factor is generally conserved along the phylogenetic scales and in different groups at the same level. This suggests that only a few species are capable of developing broad climatic tolerances, which is consistent with the fact that amphibians are generally climate and habitat specialists (Wake & Vredenburg, 2008). Furthermore, those species that evolve broad environmental tolerances may be exposed to greater competition because they may have broader distributions (Stevens, 1989). Even the family Salamandridae, which is found exclusively in the temperate region, is less rich where temperature seasonality is high. The importance of this variable in shaping richness patterns had been previously reported for fishes of the class Actinopterygii (García-Andrade et al., 2023), and its generally conserved effect was also reported along the phylogenetic scales. As such, this trait appears to be phylogenetically conserved in distantly related groups, and is likely to be the main cause preventing tropical organisms from adapting to temperate regions (reviewed in Wiens & Graham, 2005).

Although topographic complexity frequently contributed to the configuration of richness patterns in various groups analyzed here, its effect was variable, which may be due to the specific evolutionary histories of each group. For example, the family Hylidae presented a negative relationship with topographic complexity, as its areas of greatest diversity are found in the Amazon and the Atlantic Forest region in Brazil, which harbor less topographic complexity than the Appalachian region in the USA and the Andes in South America that contain lower species richness. This fact may be explained by conditions that hinder the dispersal of the group in high altitude areas, as well as the temperature seasonality that seems to limit the establishment of many species in the temperate region (Wiens et al., 2006). On the other hand, the Strabomantidae family, which is restricted to South America, has a positive relationship with topographic complexity, since its area of greatest richness is in the Andes and there are no other important mountainous regions within its range. Therefore, we might expect this group to commonly evolve adaptations that allow them to cope with high elevations, as found by Pintanel et al. (2019) for Andean *Prsitimantis* frogs.

Evolutionary time was only found to be a significant predictor of richness in salamanders, and the positive effect of this factor remained constant across the phylogenetic scales (order Caudata and families Plethodontidae and Salamandridae). This factor seems to underlie why these groups (Caudata and its families) present latitudinal patterns that are different from the other groups (Anura, Gymnophiona, and their families). For example, since Salamandridae have a temperate origin (Pyron, 2014), the positive effect of evolutionary time may be the main reason why this family shows an inverse LDG, since in this region species would have had the time to accumulate higher species richness. Another possible cause of this pattern that may act together with evolutionary time is niche conservatism, which limits the dispersal of species to other regions with environmental conditions different from those present in the ancestral region of a group (Wiens et al., 2010), and may be the main reason why this family is absent in the tropical region.

In the case of Plethodontidae, these salamanders have diversified in both the temperate and tropical regions, resulting in a bimodal LDG. This pattern may still reflect the positive effect of evolutionary time, since the origin of this family is temperate (Pyron, 2014), and one of its areas of greatest richness is in the northern temperate region. On the other hand, we found that the highest richness of this family in the tropical region is in mountainous areas, which have generally been inhabited for a longer time, thus promoting the strong effect of evolutionary time in this group. Similar results were reported by Wiens et al. (2007) who found that the highest richness of tropical Plethodontidae is at mid-elevations, which have been inhabited for a longer time. These authors also suggest that niche conservatism may limit dispersal to lower elevations, since the climate at mid-elevations is similar to that of the temperate region, and this may also be a reason why we found less richness in low-elevation areas, such as the Yucatan Peninsula.

Our study demonstrates the importance of using ecological and evolutionary factors to analyze the various hypotheses around richness patterns, as well as the interactions between these factors. Although in some groups (frogs and generally caecilians) there was no significant effect found between evolutionary factors on species richness, this does not mean that evolutionary mechanisms do not play an important role in determining richness patterns, since due to our spatial scale of analysis and the available data it was not possible to estimate extinction and dispersion rates, which are the remaining evolutionary mechanisms that can determine richness

patterns (Kozak & Wiens, 2012). However, the use of ecological factors may shed light on how evolutionary mechanisms determine richness; for example, the effect of temperature seasonality may be limiting the dispersion of tropical species into temperate regions and therefore contributing to the classic latitudinal pattern presented by most of the groups analyzed. A study that partially supports this idea is Pyron and Wiens (2013), who reported that the lower richness of amphibians in temperate areas is due (at least in part) to a limited dispersal of tropical amphibians into temperate regions. On the other hand, Wiens et al. (2006) found that temperature seasonality is the variable that best predicts the distribution limits of several tropical lineages within Hylidae. Our study also demonstrates the importance of using the deconstructive phylogenetic approach, as we were able to identify factors that are important in determining the richness of a single group; for example, evolutionary time was exclusively important in salamanders, which may explain why, unlike other groups of amphibians whose greatest richness is found in the tropics (or in tropical and southern temperate region for Gymnophiona), in this group the greatest richness is found in the northern temperate zone or is bimodally distributed (in tropical and northern temperate zone). At the class level, however, the importance of this factor is lost, as it does not represent an important factor in the other groups (approx. 90% of the entire class), causing a non-significant effect on the overall configuration of richness in Amphibia.

## 5. Conclusions

Although the direction of different factors analyzed may vary across the phylogenetic scales and in groups of the same hierarchical level, we found that temperature seasonality and canopy height are two ecological factors whose effects generally remain constant across the phylogenetic scales and between groups of the same hierarchical level in amphibians. This shows that although there may be variation in the response of some factors depending on the evolutionary history of each group (orders or families), there are others that are phylogenetically conserved and thus essential to determining the richness patterns of amphibians. On the other hand, effects of evolutionary factors were found to contribute less frequently to the richness patterns of the groups analyzed, with only evolutionary time showing a constant positive effect in Caudata and its families. The apparent lack of importance of evolutionary factors does not imply that evolutionary mechanisms do not play a role in determining the configuration of richness patterns, and further studies are recommended to implement methods such as the Geographic State Speciation and Extinction model, which quantifies extinction and dispersion rates (Goldberg et al., 2011), to better understand their importance in the configuration of richness patterns and their interaction with ecological factors.

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#### Acknowledgments

This paper is part of the requirements for RPH to obtain a Master of Sciences degree at the Posgrado en Ciencias Biológicas, UNAM, who also received a scholarship from CONAHCYT (num. 826247) during his studies. We also thank Juan Daniel Vásquez-Restrepo and Ana Berenice García-Andrade for their valuable recommendation on the R packages. JAV acknowledges funding from the Direction General de los Asuntos del Personal Académico (DGAPA) through the grant UNAM-PAPIIT IA206523.

#### Biosketch

**Rafael Peralta Hernández** is a master student at the Universidad Nacional Autónoma de México (UNAM). He is interested in the processes underlying amphibian diversity and how these vary over spatial and temporal scales.

Author contributions: JAV, RPH and LMOO conceived the ideas, FV helped to refine and contextualize them. RPH collected and analyzed the data. FV, JAV and LMOO validated the results. RPH wrote the first draft of the manuscript, and all authors contributed substantially to its revision and writing.

## Discusión general y conclusiones

El enfoque deconstructivo utilizado en este trabajo permitió analizar la importancia de diferentes variables ecológicas y evolutivas en la configuración de los patrones de riqueza de anfibios en diferentes escalas filogenéticas y en distintos grupos taxonómicos (clados) en la misma escala. Con ello, pudimos documentar que a pesar de que existe variación en la dirección del efecto de algunas de las variables estudiadas, dependiendo de la historia evolutiva particular de los clados analizados y de la escala filogenética, otras se mantienen constantes. En particular, encontramos que el efecto de las variables ecológicas tiende a mantenerse constante en las diferentes escalas analizadas y entre grupos en la misma escala, mientras que de las variables evolutivas solo el efecto del tiempo evolutivo se mantuvo constante y exclusivamente en el orden Caudata y sus familias.

El efecto relativamente constante de la altura del dosel y de la estacionalidad de la temperatura muestran la importancia de considerar factores ecológicos como determinantes de los patrones de riqueza de anfibios. Ello tiene sentido considerando que la mayoría de los anfibios son en general especialistas de hábitat y con distribuciones geográficas restringidas (Wake y Vredenburg, 2008). Por lo tanto, conforme incrementa la altura del dosel, y con ello el espacio ecológico disponible, las especies de anfibios potencialmente disponen de mayor variedad de condiciones microclimáticas, promoviéndose la coexistencia de mayor número de especies. Por otra parte, la estacionalidad de la temperatura, que implica alta variación de los valores de temperatura, puede limitar la riqueza de especies, dado que generalmente los anfibios poseen tolerancias ambientales estrechas.

Nuestros resultados rara vez mostraron efectos significativos de las variables evolutivas analizadas sobre la riqueza de especies. Sin embargo, el efecto constante del tiempo evolutivo a través del orden Caudata y sus familias merece una mención especial, ya que parece ser la razón principal por la que en este grupo se presentan patrones latitudinales inversos y bimodales con picos de riqueza en la región tropical y templada del norte que no se presentan en otros grupos. Lo anterior se puede explicar considerando que el orden Caudata y sus familias analizadas se originaron en la región templada del norte (Pyron, 2014), además de que el efecto del tiempo evolutivo en estos grupos es positivo. Por lo tanto, han tenido mayor tiempo para acumular especies en esta región a diferencia de los otros grupos que no presentan un efecto positivo del tiempo evolutivo (excepto Caeciliidae) y cuyo origen es tropical o distribuido ampliamente (Pyron, 2014).

Cabe mencionar que de las variables evolutivas que se conoce pueden modificar la riqueza de especies, no incluimos la tasa de extinción ni de dispersión (Kozak y Wiens, 2012). Ello porque la escala espacial de análisis que utilizamos no lo permite y a que es controversial estimar tasas de extinción únicamente con datos filogenéticos (Rabosky, 2010). Sin embargo, las variables ecológicas también pueden sugerir como otras variables evolutivas que no se evaluaron en este estudio pueden asociarse a la configuración de los patrones observados. Por ejemplo, cambios extremos de temperatura y fuerte estacionalidad podrían respectivamente limitar la adaptación (ocasionando extinción) y la dispersión/colonización de algunas especies, dada la especialización de hábitat y distribución restringida de los anfibios en general.

Recomendamos para futuros estudios que analicen las causas de los patrones de riqueza considerar tanto variables evolutivas como ecológicas en conjunto para determinar el rol directo de las variables evolutivas, así como el rol indirecto de las variables ecológicas a través de las

variables evolutivas. Además, en el caso que no se cuente con datos suficientes de las variables evolutivas, las variables ecológicas pueden arrojar luz sobre los mecanismos evolutivos que determinan los patrones de riqueza como lo mencionamos anteriormente. Por otro lado, este estudio demuestra como la historia evolutiva de diferentes grupos (de la misma escala filogenética o diferente) influye en la relación que presentan las variables analizadas y el patrón de riqueza. A pesar de lo anterior la relación de algunas variables con la riqueza de especies puede mantenerse constante en diferentes grupos, probablemente debido a características que evolucionaron de manera similar. Por lo tanto, recomendamos utilizar un enfoque deconstructivo filogenético o incluir diferentes taxones del mismo rango linneano, para determinar qué características de los grupos son responsables de que la riqueza responda de manera similar o no a diferentes variables.

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