



**UNIVERSIDADE ESTADUAL DE SANTA CRUZ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA
BIODIVERSIDADE**

JORGE MARIO HERRERA LOPERA

**ONDE CONSERVAR OS ANFÍBIOS? UMA AVALIAÇÃO GLOBAL DE VIESES DE
CONHECIMENTO E ÁREAS PRIORITÁRIAS SOB CENÁRIOS DE MUDANÇAS
CLIMÁTICAS**

ILHÉUS – BAHIA

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Tese apresentada à Universidade
Estadual de Santa Cruz, como
parte das exigências para obtenção
do título de Doutor em Ecologia e
Conservação da Biodiversidade.

Área de concentração: Ecologia e Conservação da
Biodiversidade

Orientador: Prof. Dr. Mirco Solé Kienle

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ILHÉUS – BAHIA

2026

H565

Herrera Lopera, Jorge Mario.

Onde conservar os anfíbios? Uma avaliação global de vieses de conhecimento e áreas prioritárias sob cenários de mudanças climáticas / Jorge Mario Herrera Lopera. – Ilhéus, BA: UESC, 2026.

200 f.:il.; anexos.

Orientador: Mirco Solé Kienle.

Tese (doutorado) – Universidade Estadual de Santa Cruz. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade.

Inclui referências.

1. Biodiversidade – Conservação. 2. Anfíbio – Conservação. 3. Mudanças climáticas. I. Título.

CDD 333.95

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Ilhéus, 09 de fevereiro de 2026

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Aos meus pais, Maritza Lopera e Jair Herrera,
tudo é sempre por vocês e para vocês.

AGRADECIMENTOS

Primeiramente, agradeço aos meus pais, Maritza Lopera Cano e José Jair Herrera, por apostarem na educação para mim e para minha irmã, sem importar os sacrifícios e incômodos que isso significasse, e por me apoiarem sempre, mesmo quando não ficava totalmente claro por que era importante "estudar sapos". À minha irmã, Laura Lucía Herrera Lopera (Mocos), por estar sempre disposta a me ouvir e me ajudar a encontrar janelas quando todas as portas pareciam fechadas.

Agradeço a Geanne Carla Novais Pereira, minha companheira e amiga. A melhor decisão da minha vida foi ter aceitado ser seu assistente de campo. Não há palavras suficientes para agradecer o que você faz por mim no dia a dia, tanto de forma pessoal, com seu amor infinito, quanto de forma profissional, com sua visão objetiva do estudo das coisas que nos apaixonam. Esta tese também é um pouco sua. Só posso agradecer por sempre me levantar quando precisei, por aquecer meu coração nos momentos em que nem o sol da Bahia era suficiente e por cuidar de mim e dos nossos bichos sempre. Te amo.

A Goya e Baleia, meus bichos: mesmo que vocês não possam ler isto, quero deixar registrado por escrito e para o mundo que cuidar de vocês no dia a dia, vê-los crescer e aprender com vocês tem sido uma das experiências mais bonitas e enriquecedoras da minha vida.

"Se enxerguei mais longe, foi porque estava sobre os ombros de gigantes", disse Newton certa vez. Se esta tese está escrita hoje, também foi porque gigantes me ajudaram a forjar minha pessoa e a encontrar o caminho de construção do meu "eu acadêmico". Portanto, é fundamental agradecer aos meus orientadores: Mirco Solé e Carlos Cultid, por fazerem muito mais do que seu dever como orientadores ditava; por saberem me motivar para ser criativo, mas também me conter para ser objetivo. Agradeço-lhes hoje e sempre por toda a ajuda nestes quatro anos de doutorado (e muito antes também).

Agradeço aos grupos de pesquisa dos quais fiz parte e dos quais atualmente faço parte, pois através da amizade e do compartilhamento e discussão com seus membros foram construídas grande parte das ideias que serviram de base para as discussões desta tese: ao Grupo de Ecologia e Diversidade de Anfíbios e Répteis (GEDAR) da Universidad de Caldas, especialmente a M. Silvana Cárdenas, Maria Fernanda Loaiza, K. Johana Molina,

Marcelo Franco e Santiago Caicedo; ao Biodiversity in Neotropical Landscape Lab do Instituto de Ecología A.C., especialmente a Andrés Guarín; ao Tropical Herpetology Lab da Universidade Estadual de Santa Cruz, especialmente a Daniel Grundmann, Gabriela Alves Ferreira, Martín Cervantes-López e Iuri Ribeiro; e ao Grupo de Macroecologia Aplicada à Conservação (GMAC).

Agradeço aos docentes da Universidad de Caldas (COL), do Instituto de Ecología A.C. (MEX) e da Universidade Estadual de Santa Cruz (BR), por abrirem minha mente e, com isso, as portas para este mundo que me faz tão feliz estudar, especialmente a Viviana Andrea Ramírez Castaño e Eduardo Pineda, que me acolheram durante a graduação e o mestrado, respectivamente. Certamente estou deixando de fora muitas pessoas importantes na minha formação acadêmica, como aqueles que contribuíram com os dados sobre os quais esta tese se constrói, ou os revisores dos trabalhos que, ao longo da minha trajetória acadêmica, forjaram minha forma de entender a ecologia e a conservação atualmente. A todos eles, peço desculpas por não mencioná-los, mas lhes agradeço profundamente. Agradeço também a Mayra e a Amáville, secretárias do PPG em Ecologia e Conservação da Biodiversidade da UESC, por estarem sempre dispostas a me ajudar e a me entender, inclusive no início do doutorado, quando a barreira do idioma dificultava a compreensão dos meus pedidos.

Agradeço ao Brasil e ao seu povo, por me abrirem suas portas, por me mostrarem um mundo diferente, por me ensinarem com paciência seu idioma, seus costumes e sua forma de ver a vida. Por me deixarem amigos maravilhosos, tantos que eu não poderia nomeá-los numa única seção, família que eu não conhecia, mas precisava conhecer, música nova que jamais sonhei gostar tanto e um amor infinito que me faz feliz todos os dias. Obrigado.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001, através de uma bolsa para estudos de doutorado (No. 88887.814811/2023-00), sem ela, esta tese e minha estadia no Brasil não teriam sido possíveis.

Finalmente, agradeço à banca que aceitou revisar esta tese: à Dra. Samanta Iop, à Dra. Camila Both, ao Dr. Mario R. Moura, ao Dr. João Carlos Pires Oliveira, à Dra. Eliana Cazetta e ao Dr. Iuri Ribeiro Dias. Meus mais profundos agradecimentos.

"For people the world over and throughout history, frogs symbolize rebirth and renewal. This association reflects three aspects of frogs' biology, one of which is their very essence: "Here today, gone tomorrow." Frogs appear from nowhere following a hard rain and then disappear. In temperate areas, they emerge with warmer spring temperatures and vanish in the fall when temperatures plummet... Second, frogs symbolize rebirth because periodically they slough their outermost layer of skin, revealing a fresh skin underneath... Third, frogs symbolize rebirth because many species experience a "magical" metamorphosis: transformation from an aquatic, gill-breathing, swimming tadpole into a terrestrial, lung-breathing, leaping frog. We are fascinated with frog metamorphosis, perhaps because the change parallels our own transition from fetus bathed in amniotic fluids to baby's entry to the outside world. Just as frogs, we also pass through critical stages in our lives..."

"Para as pessoas do mundo todo e ao longo da história, os sapos simbolizam renascimento e renovação. Essa associação reflete três aspectos da biologia dos sapos, um dos quais é sua própria essência: "Hoje aqui, amanhã já não". Os sapos aparecem do nada após uma chuva forte e depois desaparecem. Em áreas temperadas, eles emergem com as temperaturas mais quentes da primavera e desaparecem no outono, quando as temperaturas caem... Em segundo lugar, os sapos simbolizam o renascimento porque periodicamente trocam a camada mais externa da pele, revelando uma pele nova por baixo... Em terceiro lugar, os sapos simbolizam o renascimento porque muitas espécies passam por uma metamorfose "mágica": a transformação de um girino aquático, que respira por guelras e nada, em um sapo terrestre, que respira por pulmões e salta. Somos fascinados pela metamorfose dos sapos, talvez porque a mudança seja paralela à nossa própria transição de feto banhado em líquido amniótico para a entrada do bebê no mundo exterior. Assim como os sapos, também passamos por fases críticas em nossas vidas..."

Marty Crump,

Eye of newt and toe of frog, adder's fork and lizard's leg: the lore and mythology of amphibians and reptiles, 2015.

Resumo

Os anfíbios constituem atualmente o grupo de vertebrados mais ameaçado, com mais de 40% de suas espécies classificadas em alguma categoria de risco. A perda de habitat é a principal causa da redução das populações de anfíbios em escala global. Nesse contexto, a criação de áreas protegidas parece ser a estratégia mais adequada para sua conservação. No entanto, diversos desafios limitam a proteção eficaz dos anfíbios por meio das áreas protegidas. Primeiro, a distribuição espacial conhecida das espécies apresenta fortes vieses amostrais, como já documentado para vários grupos biológicos. Segundo, as áreas protegidas existentes não foram originalmente planejadas para proteger a “diversidade” em um sentido amplo, mas sim para resguardar espécies focais ou padrões de riqueza, desconsiderando dimensões fundamentais para o funcionamento dos ecossistemas, como funções ecológicas e histórias evolutivas. Terceiro, as mudanças climáticas podem alterar substancialmente a distribuição das espécies devido a modificações em temperatura, precipitação e outras variáveis ambientais. Nesta tese, abordamos essas questões ao longo de três capítulos, com o objetivo de gerar informações úteis para apoiar decisões relacionadas à conectividade e à criação de áreas protegidas, em consonância com acordos internacionais como o Kunming–Montreal Global Biodiversity Framework, que tem como meta proteger 30% da área terrestre até 2030 e promovendo uma conservação mais abrangente da diversidade de anfíbios. Primeiro, avaliamos o nível de completude do registro global de anfíbios, identificando regiões onde é necessário direcionar esforços para reduzir vieses espaciais no conhecimento de sua distribuição. No segundo capítulo, utilizando dados espaciais e atributos funcionais e filogenéticos, identificamos globalmente as áreas com maior diversidade alfa e beta multidimensional, que deveriam ser prioritárias para o planejamento da conservação. Por fim, no terceiro capítulo aplicamos a mesma abordagem para prever como essas áreas de alta diversidade podem mudar sob diferentes cenários climáticos, permitindo identificar zonas estáveis que permanecerão prioritárias mesmo frente às mudanças climáticas. Nos três capítulos comparamos os resultados com a distribuição atual das áreas protegidas para avaliar o grau de sobreposição e indicar regiões onde há maior necessidade de investimento na criação e ampliação de áreas protegidas. Longe de

encerrar o tema, esta tese abre caminho para novas perguntas, análises em outras escalas espaciais, temporais e taxonômicas e para a aplicação de um protocolo replicável a outros grupos biológicos.

Palavras chave. Conservação de Anfíbios; Planejamento de Conservação; Lacunas de Conhecimento; Diversidade Multidimensional; Mudanças Climáticas.

Abstract

Amphibians currently constitute the most threatened group of vertebrates, with over 40% of their species classified under some risk category. Habitat loss is the primary cause of global amphibian population declines. In this context, the establishment of protected areas appears to be the most suitable conservation strategy. However, several challenges limit the effective protection of amphibians through protected areas. First, the known spatial distribution of species exhibits strong sampling biases, as already documented for various biological groups. Second, existing protected areas were not originally designed to protect "diversity" in a broad sense, but rather to safeguard focal species or patterns of species richness, overlooking fundamental dimensions for ecosystem functioning such as ecological functions and evolutionary histories. Third, climate change can substantially alter species distributions due to changes in temperature, precipitation, and other environmental variables. In this thesis, we address these issues across three chapters, aiming to generate useful information to support decisions related to connectivity and the creation of protected areas, in line with international agreements such as the Kunming-Montreal Global Biodiversity Framework, which aims to protect 30% of terrestrial areas by 2030 and promote more comprehensive conservation of amphibian diversity. First, we assess the completeness of the global amphibian record, identifying regions where efforts should be directed to reduce spatial biases in knowledge of their distribution. In the second chapter, using spatial data alongside functional and phylogenetic attributes, we globally identify areas with the highest multidimensional alpha and beta diversity, which should be prioritized for conservation planning. Finally, in the third chapter, we apply the same approach to predict how these high-diversity areas may shift under different climate scenarios, allowing us to identify stable zones that will remain priorities even in the face of climate change. In all three chapters, we compare the results with the current distribution of protected areas to evaluate the degree of overlap and indicate regions with the greatest need for investment in establishing and expanding protected areas. Far from concluding the subject, this thesis paves the way for new questions, analyses at different spatial, temporal, and taxonomic scales, and the application of a replicable protocol to other biological groups.

Keywords. Amphibian Conservation; Conservation Planning; Knowledge Gaps; Multidimensional Diversity; Climate Change.

Resumen

Los anfibios constituyen actualmente el grupo de vertebrados más amenazado, con más del 40% de sus especies clasificadas en alguna categoría de riesgo. La pérdida de hábitat es la principal causa de la reducción de las poblaciones de anfibios a escala global. En este contexto, la creación de áreas protegidas parece ser la estrategia más adecuada para su conservación. Sin embargo, diversos desafíos limitan la protección efectiva de los anfibios mediante áreas protegidas. En primer lugar, la distribución espacial conocida de las especies presenta fuertes sesgos de muestreo, como ya se ha documentado para varios grupos biológicos. En segundo lugar, las áreas protegidas existentes no fueron planificadas originalmente para proteger la "diversidad" en un sentido amplio, sino para resguardar especies focales o patrones de riqueza, desconsiderando dimensiones fundamentales para el funcionamiento de los ecosistemas, como las funciones ecológicas y las historias evolutivas. En tercer lugar, los cambios climáticos pueden alterar sustancialmente la distribución de las especies debido a modificaciones en la temperatura, la precipitación y otras variables ambientales. En esta tesis, abordamos estas cuestiones a lo largo de tres capítulos, con el objetivo de generar información útil para apoyar decisiones relacionadas con la conectividad y la creación de áreas protegidas, en consonancia con acuerdos internacionales como el Marco Global de Biodiversidad Kunming-Montreal, que tiene como meta proteger el 30% del área terrestre para 2030 y promover una conservación más integral de la diversidad de anfibios. Primero, evaluamos el nivel de completitud del registro global de anfibios, identificando regiones donde es necesario dirigir esfuerzos para reducir sesgos espaciales en el conocimiento de su distribución. En el segundo capítulo, utilizando datos espaciales y atributos funcionales y filogenéticos, identificamos a nivel global las áreas con mayor diversidad alfa y beta multidimensional, que deberían ser prioritarias para la planificación de la conservación. Finalmente, en el tercer capítulo aplicamos el mismo enfoque para predecir cómo estas áreas de alta diversidad pueden cambiar bajo diferentes escenarios climáticos, permitiendo identificar zonas estables que permanecerán prioritarias incluso frente a los cambios climáticos. En los tres capítulos comparamos los resultados con la distribución actual de las áreas protegidas para evaluar el grado

de superposición e indicar regiones donde existe mayor necesidad de inversión en la creación y ampliación de áreas protegidas. Lejos de cerrar el tema, esta tesis abre camino a nuevas preguntas, análisis en otras escalas espaciales, temporales y taxonómicas, y a la aplicación de un protocolo replicable a otros grupos biológicos.

Palabras clave. Conservación de Anfibios; Planificación de la Conservación; Lagunas de Conocimiento; Diversidad Multidimensional; Cambio Climático.

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Introdução geral

Os anfíbios representam um dos grupos de vertebrados mais antigos, com uma história evolutiva que ultrapassa 290 milhões de anos (Vitt & Caldwell, 2014). Atualmente, são reconhecidas pouco mais de 8.975 espécies distribuídas em três clados: Anura, que inclui rãs, sapos e pererecas e concentra a maior parte da diversidade do grupo (7.908 espécies; 88,11% do total); Caudata, composto por salamandras, axolotes e tritões (836 espécies; 9,31%); e Gymnophiona, formado pelas cecílias ou cobras-cegas (231 espécies; 2,57%) (Frost, 2025).

A diversidade morfológica e ecológica dos Anfíbios se reflete na sua grande variedade de estratégias de vida e de interações ecológicas. Existem espécies essencialmente aquáticas; outras são fossoriais, vivendo a maior parte do tempo sob o solo; algumas exploram o ambiente terrestre, utilizando a serrapilheira e corpos d'água temporários; enquanto certos grupos, como os Terrarana, depositam seus ovos diretamente na serapilheira, originando juvenis totalmente desenvolvidos, sem estágio larval aquático. Outras espécies ocupam o estrato arbóreo, e diversas rãs de dossel utilizam água acumulada em bromélias e axilas das árvores (fitotelmatas) para sua reprodução, evitando o retorno ao solo (Duellman & Trueb, 1994; Pough, 2016). Essa diversidade de uso de micro-habitats resulta em uma rede complexa de interações ecológicas. Os anfíbios atuam simultaneamente como predadores e presas, conectando níveis tróficos e contribuindo para o fluxo de energia e o funcionamento dos ecossistemas (Caicedo-Martínez et al., 2021, 2025; Cárdenas-Ortega & Cárdenas-Ortega, 2022; Pough, 2016). Além de sua importância ecológica, os anfíbios têm desempenhado papéis simbólicos profundos nas culturas humanas ao longo do tempo. Em múltiplas culturas lhes foram atribuídos poderes sobrenaturais, desde explicações para eclipses até símbolos de sorte ou transformação, e seu ciclo de vida,

marcado por longos períodos de aparente ausência e emergências explosivas após as chuvas, inspirou associações com fertilidade, ressurreição, imortalidade e criação homem ou do mundo em diferentes tradições (Crump, 2015).

A pesar da sua relevância ecológica e evolutiva, os anfíbios estão entre os grupos de vertebrados mais ameaçados do planeta. Estima-se que cerca de 41% das espécies se encontrem em alguma categoria de ameaça (IUCN, 2024). A perda e fragmentação de habitat, impulsionadas pela expansão da fronteira agrícola, urbanização e mudanças no uso do solo, constituem a principal ameaça global (Luedtke et al., 2023). Adicionalmente, as mudanças climáticas vêm alterando os regimes de temperatura e precipitação, comprometendo a adequabilidade ambiental de muitas espécies e aumentando a frequência e intensidade de eventos extremos (Rosenfield et al., 2025; Wake & Vredenburg, 2008). A estas ameaças soma-se a propagação de doenças emergentes, como a quitridiomicose, causada pelo fungo *Batrachochytrium dendrobatidis*, que tem levado populações inteiras ao colapso em diversas regiões do mundo (IUCN SSC Amphibian Specialist Group, 2024). Tais ameaças atuam de forma sinérgica, amplificando os efeitos umas das outras e tornando ainda mais urgente a implementação de estratégias de conservação eficazes. Diante desse cenário, a estratégia mais direta e eficaz para favorecer a conservação dos anfíbios é a proteção de seus habitats, especialmente por meio da criação, conectividade e fortalecimento de áreas protegidas (APs) (Araújo et al., 2006; Watson et al., 2014, 2016).

As áreas protegidas tiveram origens variadas ao redor do mundo. Em alguns lugares surgiram como reservas de caça, em outros, como reservas de fontes hídricas ou espaços destinados ao desfrute das paisagens naturais (Chape et al., 2008). No

entanto, no âmbito dos acordos internacionais atuais, um dos papéis fundamentais das APs é proteger a biodiversidade (Quan et al., 2018; Watson et al., 2016). O Acordo de Kunming–Montreal é um acordo internacional ao qual cerca de 196 países ao redor do mundo aderiram; entre suas metas está a proteção de pelo menos 30% da superfície terrestre, com a intenção de proteger a “biodiversidade, funções e serviços ecossistêmicos” (Kunming-Montreal Global Biodiversity Framework, 2022). Aqui, é importante definir o conceito de biodiversidade. Solbrig (1991), em um documento para a UNESCO, por exemplo, definiu biodiversidade como “a propriedade dos grupos de entidades vivas de serem variados”, entendendo que essa variação não ocorre apenas em seus nomes ou identidades (espécies, diversidade taxonômica), mas também no que fazem (funções, diversidade funcional) e em sua história evolutiva (linhagens, diversidade filogenética). Dessa forma, o fortalecimento das APs não pode basear-se unicamente em critérios de riqueza de espécies, nem exclusivamente na distribuição de espécies ameaçadas, que não desempenham papéis ecossistêmicos diferenciados em relação às espécies não ameaçadas (González-del-Piego et al., 2024; González-Gutiérrez et al., 2025), mas exige a integração de diferentes dimensões da possível variação dos organismos, uma vez que esta é a única maneira de nos aproximarmos do objetivo de conservar a biodiversidade desses grupos (Hannah et al., 2007; Quan et al., 2018). Adicionalmente, não vivemos em um mundo estático; o avanço das mudanças climáticas altera as condições ambientais e compromete a persistência dos anfíbios nos ecossistemas onde atualmente ocorrem, criando a necessidade de que as APs, além de integrarem a biodiversidade atual, funcionem como refúgios climáticos sob futuros cenários de mudança (Hannah et al., 2007; Rosenfield et al., 2025; Wake & Vredenburg, 2008).

Apesar dos avanços no conhecimento sobre a diversidade e distribuição dos anfíbios, persistem importantes lacunas que limitam a eficácia das ações de conservação. Em primeiro lugar, o conhecimento sobre a distribuição das espécies é marcado por fortes vieses amostrais: extensas regiões permanecem subamostradas ou completamente inexploradas, enquanto outras concentram esforços de coleta desproporcionais (Herrera-Lopera et al., 2025). Em segundo lugar, a maioria dos estudos de priorização espacial tem se baseado exclusivamente na riqueza de espécies ou na distribuição de espécies ameaçadas, ignorando outras dimensões da biodiversidade, como a diversidade funcional e filogenética, que capturam aspectos complementares do valor biológico das áreas (Quan et al., 2018). Por fim, as projeções sobre os efeitos das mudanças climáticas na diversidade multidimensional futura dos anfíbios em grande escala ainda são escassas e, quando existem, raramente incorporam a incerteza associada a diferentes cenários socioeconômicos e modelos climáticos (Alves-Ferreira et al., 2025).

Diante da necessidade de fornecer aos tomadores de decisão ferramentas que permitam identificar os locais prioritários para destinar os recursos limitados (Borzée et al., 2025) para conservação, reduzir lacunas de informação e conservar áreas altamente biodiversas no presente que permaneçam biodiversas no futuro, apresentamos esta tese. Em três capítulos, abordamos a identificação de lacunas de informação e vieses na completude amostral de anfíbios em escala global (capítulo 1), as áreas com maior biodiversidade multidimensional de anfíbios em escala global no presente (capítulo 2) e as áreas biodiversas que se manterão biodiversas (i.e., que se manterão estáveis) frente a diferentes cenários climáticos futuros (capítulo 3). Esperamos que este trabalho, mais do que encerrar debates, estimule novas

perguntas e caminhos para a conservação *in situ* dos anfíbios em múltiplas escalas espaciais e temporais.

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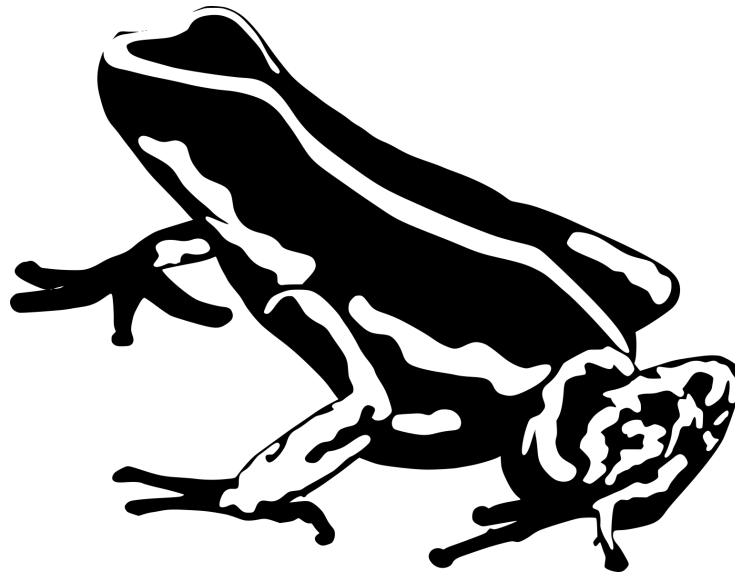
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Capítulo 1

Mapping the missing: assessing amphibian sampling completeness and overlap with global protected areas

Artigo publicado em Ecology and Evolution

DOI: 10.1002/ece3.71137



Phyllobates lugubris – Gabriela Palomo-Munoz

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*"We can't care about protecting what we don't know,
and we can't know what we haven't experienced".*

*"Não podemos nos preocupar em proteger o que não conhecemos,
e não podemos conhecer o que não vivenciamos".*

- Marty Crump

Mapping the missing: assessing amphibian sampling completeness and overlap with global protected areas

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Acknowledgements

We thank Karoline Cerón, Nicolás Urbina and Michel Varajão Garey, for their valuable comments and constructive feedback, which greatly contributed to the improvement of this work from its initial version.

Mapping amphibian data-gaps: global assessment of sampling completeness and overlap with protected and key biodiversity areas

Abstract

Aim. Assess amphibian sampling completeness and the overlap of sampling completeness categories with natural protected areas (NPAs) and key biodiversity areas (KBAs).

Location. Global level.

Time period. Not applicable.

Major taxa studied. Amphibians.

Methods. We evaluated amphibian sampling completeness across six of the Earth's eight biogeographic realms to identify *well-sampled*, *under-sampled*, and *data-gap* areas in the context of global amphibian distribution. Additionally, we examined the spatial overlap of each sampling category with Natural Protected Areas (NPAs) and Key Biodiversity Areas (KBAs).

Results. The Nearctic and Australasian realms had the highest number of records and well-sampled areas. Significant data gaps were identified particularly in the Afrotropical, Indo-Malayan, Neotropical, and Palearctic realms. We found low levels of spatial match (< 35%) between classified areas and NPAs/KBAs.

Main conclusions. Amphibian distribution data is largely incomplete, with the most extensive gaps in the most species-rich realms: Neotropic, Indo-Malayan, and Afrotropical. The low overlap between under-sampled and data-gap areas with NPAs and KBAs suggests that these regions, critical for amphibian diversity, are insufficiently represented within established conservation priorities. Given the urgent threats to biodiversity from global change, rapid responses are essential to enhance our

understanding of species distributions and community structure in amphibians. This study provides spatial insights to help identify key data-gap areas for amphibian research and conservation prioritization.

Key words. Amphibian Conservation, Research Prioritization, Distribution Data Gaps, Key Biodiversity Areas, Natural Protected Areas, Sampling Completeness.

Introduction

Amphibians are the most threatened vertebrate group, with more than 40% of their species under some threat category (IUCN, 2024a; Luedtke et al., 2023; Silva et al., 2020). Habitat loss, emerging diseases, climate change and interactions among these factors are the main causes of global decline in amphibian populations (Wake, 1991; Wake and Vredenburg, 2008). In addition, although amphibians are one of the groups for which most human and economic capital is allocated (Cardoso et al. 2011; however, see IUCN SSC, 2022), knowledge about many basic aspects of amphibian biology is incipient. For example, between 2010 and 2020, about 20% of the currently recognized species were described, and the rate of description continues to increase (Frost 2023 - Comparing amphibian richness of 5.3 and 6.0 versions). There is also a taxonomic bias in the ecological knowledge of amphibians (Silva et al., 2020): for most species, aspects such as responses to environmental pressures, natural history and distribution are still unknown (Nori et al., 2023).

Understanding how and where species are distributed is fundamental in order to formulate efficient strategies for their conservation at a global scale (Mi et al., 2023; Nori et al., 2023; Serrano et al., 2023). However, the knowledge available on amphibian distribution is taxonomically and geographically biased, under-representing species with cryptic habits (e.g., fossorial or canopy-dwelling species) while reporting a higher number of records for more conspicuous species (Hughes et al., 2021; Martin et al., 2012; Silva et al., 2020). Additionally, most records across biological groups are concentrated mainly in North America and Europe, despite the highest species richness being found in tropical regions (Girardello et al., 2019; Hughes et al., 2021; Martin et al., 2012; Pelayo-Villamil et al., 2018; Vitt and Caldwell, 2014). The recognition of this geographic bias allows the identification of priority areas for directing

research resources. Campbell Grant et al. (2023) emphasized an essential aspect of amphibian conservation: the urgent need to determine both the number and identity of species protected within Natural Protected Areas (NPAs). With human impacts increasingly altering natural systems, NPAs serve as the primary approach for in situ biodiversity conservation. Furthermore, in the face of global change, NPAs are expected to act as "*stepping stones*", supporting species as they navigate future environmental challenges (Thomas and Gillingham, 2015; Watson et al., 2016, 2014). Mi et al., (2023) found that most amphibian species are recorded in at least one Natural Protected Area (NPA). However, having a record within an NPA does not guarantee effective conservation for a species, since large portions of their distribution range remain unprotected (Mi et al., 2023) or unknown, and it is uncertain whether the populations within NPAs are viable for long-term survival. Therefore, it is essential to understand the completeness of our current knowledge to accurately assess the "actual distribution" of amphibian species (i.e., distribution based on specimen records rather than inferred from the area of occurrence or areas of occupancy) and their presence within protected areas. This clarity will also help prioritize efforts to fill information gaps, refining our ability to make informed conservation decisions.

Sampling completeness is understood as the ratio between observed species and expected species for a region and is a useful tool to determine areas where it is necessary to increase sampling effort (Chao et al., 2020; Lobo et al., 2018), in this case, to improve efforts to collect data related to amphibian distribution. Assessing and mapping areas with low data completeness and significant information gaps on a global scale aligns with the goals of the Convention on Biological Diversity (CBD) and its "2030 Targets" under the Kunming-Montreal Global Biodiversity Framework

(KMGBF), to which over 200 countries are committed (Kunming-Montreal Global Biodiversity Framework, 2022; Plumptre et al., 2024). One key target of this framework aims to “conserve 30% of land, waters, and seas” by 2030, serving as an update to the Aichi Targets (Butchart et al., 2015; CBD, 2010; Plumptre et al., 2024; Santini et al., 2016). Providing spatially explicit data on areas lacking amphibian distribution information (i.e., regions with low data completeness or no data at all) can greatly support decision-makers in directing resources to priority research areas. This targeted research will help determine whether these areas are suitable as potential expansion and connectivity zones for existing Natural Protected Areas (NPAs) worldwide. Additionally, Key Biodiversity Areas (KBAs) complement NPAs by identifying critical ecosystems that support vulnerable populations and should be preserved due to their ecological significance and integrity (IUCN, 2016). Although KBAs are not officially classified as NPAs, they play a crucial role in site-based conservation efforts led by governments and the private sector (IUCN, 2016; Plumptre et al., 2024). Identifying gaps in amphibian distribution data can help refine the designation of KBAs and therefore to strengthen site-based conservation initiatives.

The Global Biodiversity Information Facility (GBIF) is the most comprehensive open database of biological records on a global scale (Girardello et al. 2019), besides the IUCN spatial data. The difference between GBIF and IUCN spatial data is that the former consists mainly of records in georeferenced points format, while the IUCN provides distribution polygons for species, which are often interpretations of GBIF data interpreted by experts (Boitani et al., 2011). Therefore, GBIF data is likely to have fewer co-omission errors than IUCN data, and IUCN data may underestimate areas with gaps in distribution information by assuming species distributions in areas where no data are

available – due to the use of polygons (IUCN, 2024b). The GBIF brings records from different sources, such as articles, museum collections, citizen records, among others. Some authors have proposed that records in the GBIF, (especially those coming from citizens' contributions) might exhibit misidentification issues and bias: areas of higher human population density correlating with number of species records (Girardello et al., 2019; Hughes et al., 2021; Shirey et al., 2021). The use of GBIF databases for ecological research has also been criticized because they combine information from different sources with a sampling effort that is not comparable with each other (see Lobo, 2008). However, approaches of Lobo (2008) and Lobo et al. (2018) allow the use of this heterogeneous source resource as raw material for estimating completeness and identifying areas with information gaps and areas without information in simple and comparable units.

This study aimed to assess and pinpoint areas worldwide characterized by information gaps in the distribution of amphibians, highlighting the situation for each of the biogeographical realms. Our questions were: (i) where are the well-sampled, under-sampled, and data-gap areas for amphibian distribution globally?; and (ii) what level of spatial coincidence do well-sampled, under-sampled, and data-gap areas have with currently designated Natural Protected Areas (NPAs) and Key Biodiversity Areas (KBAs) on a global scale? We aim to provide valuable, clear, and spatially explicit information that identifies areas with data gaps in the global understanding of amphibian distribution.

Methods

Data regionalization

We follow Olson et al. (2001) biogeographic proposal modified by Dinerstein et al. (2017), which divides the globe in eight biogeographic realms and 14 biomes. These realms are: Afrotropic, Antarctic, Australasian, Indo-Malayan, Nearctic, Neotropic, Oceania, and Palearctic. To select a biogeographic framework, we compared this approach with that of Holt et al. (2013) and found that both frameworks are equally suitable for dividing amphibian distributions at a global scale (see Supplementary Information 1). However, we choose Olson et al. (2001) - Dinerstein et al. (2017) because it allows for the analysis of information gaps at the biome level. Although a biome-level analysis is not one of our primary objectives, we included it as an additional analysis in Supplementary Information 2. It is important to note that the Antarctic and Oceania realms were excluded from the study, as amphibians are absent in Antarctic and most oceanic islands lack amphibian species (Vitt and Caldwell, 2014) and that just a small portion of the records deposited in GBIF, after data curation, were from Oceania realm (0.03%, ~ 75 records).

We excluded areas without amphibian distribution data according to the IUCN spatial data (IUCN, 2024c) to avoid overestimating information gap areas. While some GBIF records fall within these excluded regions, aligning our analysis with the expert-informed IUCN distribution polygons provides a standardized approach. Although this method may introduce expert bias, potentially underestimating information gaps by inferring species presence in areas lacking explicit records, it offers a uniform basis for delineating species ranges and identifying unrepresented regions.

Amphibian global occurrence records

We utilized amphibian records from the Global Biodiversity Information Facility (GBIF) and the *rgbif* package in R to extract records associated with museum vouchers,

thereby minimizing the potential for misidentification (Chamberlain et al., 2023; Daru and Rodriguez, 2023; GBIF.Org, 2024; R Core Team, 2023). The records were curated using functions of the *scrubr* and *CoordinateCleaner* R packages (Chamberlain, 2022; R Core Team, 2023; Zizka et al., 2019). Given the heterogeneity of GBIF data sources and the lack of assurance that they originate from surveys with comparable sampling effort, duplicate records—defined as entries for the same species at identical latitude-longitude coordinates—were removed unless they represented different collection years, since we used collection years as surrogates in the estimation of sampling completeness (Lobo, 2008; Lobo et al., 2018). Taxonomy of records was updated and corrected using the functions and databases stored in the *AmphiNom* R package (Liedtke, 2019; R Core Team, 2023), which is grounded in the “Amphibian Species of the World 6.2” database from the American Museum of Natural History (Frost, 2024). Taxonomic information is updated to April 2024. Given the large number of records used in this study, and because species distribution polygons do not necessarily align with the available GBIF records, we aimed to minimize misidentified points by performing the data curation steps described above.

Natural Protected Areas and Key Biodiversity Areas

The polygons for Natural Protected Areas (NPAs) were obtained from The World Database on Protected Areas (WDPA - August 2023 version), which comprises the largest global database of terrestrial and marine NPAs. The database includes national and international conservation areas defined by governments as well as other effective area-based conservation measures (OECMs). Thus, National Parks, Habitat Reserves, Indigenous Reserves, Ramsar Areas, among many others, are also

considered. The polygons can be freely downloaded from *protectedplanet.net* (see UNEP-WCMC & IUCN, 2023).

The Key Biodiversity Areas (KBAs) were obtained upon request from www.keybiodiversityareas.org (BirdLife International, 2024), we used the March 2024 version.

Data analysis

To evaluate the amphibian sampling completeness at global level we used the *KnowBR* package of the R language (Lobo et al., 2018; R Core Team, 2023). The package has the advantage of allowing the use of records collected with different methodological approaches for the completeness estimation, as is the case with GBIF data which come from different types of studies (Lobo, 2008; Lobo et al., 2018; Pelayo-Villamil et al., 2018). The package requires "event – independent" records of the species as "surrogates" for the calculation of completeness (see Lobo, 2008). Therefore, we considered records with different collection years (column "year" in the GBIF data) as event-independent data.

To assess completeness levels within each realm, we divided each realm into hexagonal polygons with a width of 2 degrees (~ 222.64 km at equator) and calculated completeness for each polygon. Although we considered other resolutions, our analysis revealed a low effect size of hexagon size on completeness ($\omega^2 = 0.007$; see Supplementary Information 3). Consequently, we opted to use the 2-degree resolution, as it maximizes species richness while minimizing species co-omission.

For the calculation of completeness through the *KnowBR* package, we used the following parameters: (i) rational curve, because we had no basis for assuming an established model of density distribution or accumulation curve for amphibians, (ii)

exact Ugland et al. (2003) estimator, since we were interested in a precise estimate rather than the variation intervals in the estimate, and (iii) a minimum ratio of 1 ("*cutoff*" in the function) to ensure that there were more records than species within each of the hexagons (Lobo et al., 2018; Pelayo-Villamil et al., 2018).

To understand the variation in sampling completeness among realms, we compared the confidence intervals of completeness for each realm (Cumming et al., 2007).

Lobo et al. (2018) and Pelayo-Villamil et al. (2018), recommend classifying the sampling completeness values into three categories to get the survey quality: (i) *poor*, when sampling completeness is $< 50\%$, the ratio between species and records is < 3 and the slope value in the estimated accumulation curve is > 0.3 , (ii) *good*, when sampling completeness is $> 90\%$, the ratio between species and records is > 15 and the slope value in the estimated accumulation curve is < 0.02 and (iii) *fair*, for values in the middle. Since these values are defined by default and in the majority of studies where these criteria have been applied are at administrative division scale, where criteria such as the ratio between records and species can be more easily achieved than in cells of smaller size, we decided to modify the criteria. We adjusted them according to the proposals of Yang et al. (2013) and Girardello et al. (2018). They justify their classification criteria on the slope value of the estimated accumulation curve, since the slope is a reflection of the saturation of the curve and can be interpreted as the "*probability of discovering new species when sampling continue*", therefore, the slope should be a more accurate classification criterion than the sampling completeness value itself. They consider a slope value ≤ 0.05 as "well sampled" and slopes > 0.05 as "undersampled". Thus we decided to define three categories: (i) "*well-*

sampled", with slope ≤ 0.05 , (ii) "*under-sampled*", with slope > 0.05 , and (iii) "*data-gap*", for areas where species records should exist according to the IUCN (2024b) spatial data, but where sampling completeness could not be calculated due to insufficient records, (i.e., record-to-species ratio of ≤ 1).

To assess the percentage of spatial congruence between the classified zones and the Natural Protected Areas (NPAs) and Key Biodiversity Areas (KBAs) for each realm, we calculated the percentage of spatial match (Nori et al. 2020). This was done by overlaying the vector layers and calculating the overlapping area, then dividing this by the total area for each classified zone. The analysis was carried using *terra* and *tyditerra* R packages (Hernangómez, 2023; Hijmans, 2024; R Core Team, 2023). All calculations were performed using a global equal-area projection (Eckert IV, ESRI:54012) to preserve the true size of spatial features (i.e., hexagons, NPAs and KBAs) worldwide.

Results

Records

A total of 2,239,932 occurrence records were downloaded and curated from the GBIF. After curating the data, we retained 246,384 unique locality-years records across 73 families, 509 genera and 4891 species. The Nearctic realm contained most of the records (52.8%), followed by the Neotropical (23.9%) and Australasian realms (10.1%), while each of the remaining realms accounted for less than 10% (Figure 1, see precise numbers in Table 1).

Table 1. Records, species, genera and families of amphibians included in this study by realm.

Realm	Records – number (%)	Species – number (%)	Genera – number (%)	Families – number (%)
Afrotropic	17558 (7.13)	819 (16.75)	104 (20.43)	22 (30.14)

Australasia	24841 (10.08)	384 (7.85)	53 (10.41)	10 (13.7)
Indo-Malayan	8247 (3.35)	662 (13.54)	104 (20.43)	17 (23.29)
Nearctic	130204 (52.85)	419 (8.57)	74 (14.54)	26 (35.62)
Neotropic	58871 (23.89)	2594 (53.04)	228 (44.79)	40 (54.79)
Palaearctic	6663 (2.7)	275 (5.62)	80 (15.72)	19 (26.03)
Total	246384 (100)	4891 (100)	509 (100)	73 (100)

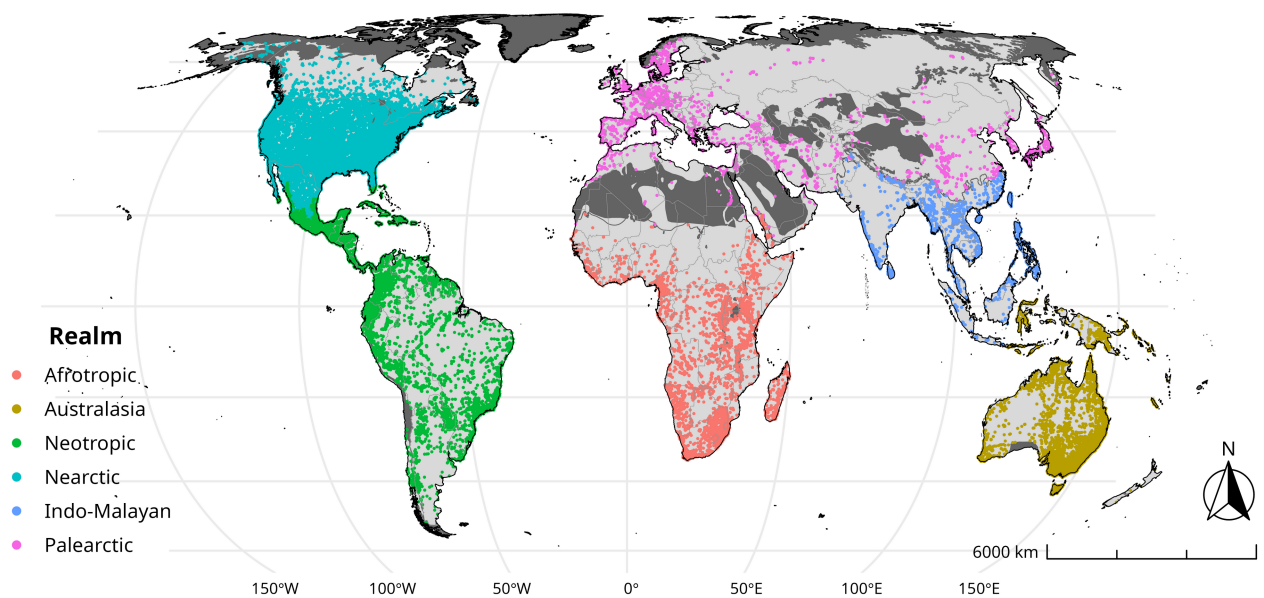


Figure 1. Curated GBIF amphibian records. Dark gray shows non-included areas due to the absence of amphibian species distribution, according to the IUCN (2024b) spatial data. Light gray represents the geographic extent of this work lacking records. Datum: Eckert IV projection, EPSG:54012.

Sampling completeness

The proportion of the area for which sampling completeness could be estimated (i.e., under-sampled and well-sampled areas), varied across realms. In the Nearctic realm, sampling completeness could be calculated for 65% of the area, followed by the Australasian realm (63%) and the Neotropical realm (55%). The Palaearctic realm had

the lowest proportion of area with estimated completeness, at only 12%. Consequently, the Palearctic was the realm with the largest amount of data-gaps, with 88% of its area within this category (Table 2).

Table 2. Proportion of areas in each sampling quality category for amphibian distributions across realms. Areas are presented in million hectares (Mha). Percentages were calculated as the area of each category divided by the total area of each realm, multiplied by 100. *ws*: Well-sampled, *Us*: Under-sampled, *Dg*: Data-gap.

Realm	Total area	ws – area (%)	Us – Area (%)	Dg – Area (%)
Afrotropic	2164.56	53.92 (2.49)	909.59 (42.02)	1201.05 (55.49)
Australasia	904.95	188.27 (20.8)	381.87 (42.2)	334.81 (37)
Indo-Malayan	848.39	12.36 (1.46)	325.04 (38.31)	510.99 (60.23)
Nearctic	1576.08	627.5 (39.81)	402.69 (25.55)	545.89 (34.64)
Neotropic	1887.44	128.72 (6.82)	909.03 (48.16)	849.69 (45.02)
Palearctic	3809.94	81.07 (2.13)	379.7 (9.97)	3349.17 (87.91)

The average completeness for hexagons differed between realms. The Nearctic realm (mean: 77.5%, 95%CI: 75.8% - 79.2%) and Australasia (mean: 65%, 95%CI: 61.8% - 68.2%) exhibited the highest levels of average sampling completeness. In contrast, the realms with the lowest average completeness were Afrotropical (mean: 47%, 95%CI: 44.5% - 49.5%), Indo-Malayan (mean: 49.7%, 95%CI: 46.2% - 53.2%), and Neotropical (mean: 47.9%, 95%CI: 45.2% - 50.6%). The Palearctic realm (mean: 54.3%, 95%CI: 51.1% - 57.5%) showed significantly lower average completeness than the Nearctic and Australasia, but higher than the Afrotropical and Neotropical, and not significantly different from the Indo-Malayan realm (Figure 2, Supplementary Information 4).

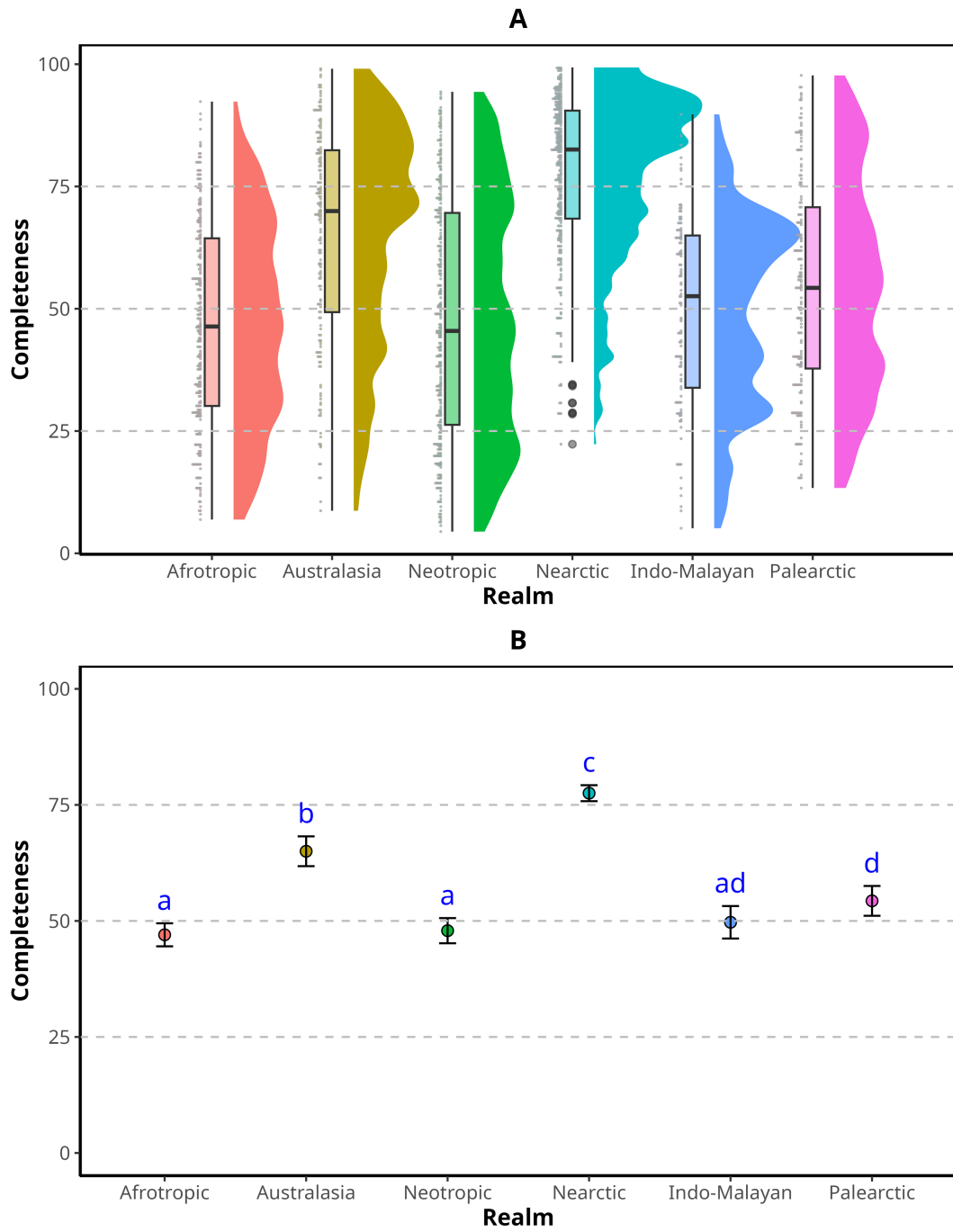


Figure 2. Estimated sampling completeness for amphibians distribution between realms. **A.** Density distribution of completeness values and **B.** Mean and 95% confidence intervals of completeness between realms, different letters represent a non-overlap of the confidence intervals.

The Nearctic realm had the highest proportion of well-sampled areas (ws: 0.4, us: 0.26, dg: 0.35), followed by Australasia (ws: 0.21, us: 0.42, dg: 0.37) and Neotropic (ws: 6.82, us: 48.16, dg: 45.02). In these three realms, the combined proportion of well-sampled and under-sampled areas exceeded that of data-gap areas. For all other realms, the proportion of data-gap areas was greater, indicating that most of the realms lacked sufficient information to make reliable calculations of sampling completeness (Table 2, Figure 3, Supplementary Information 4).

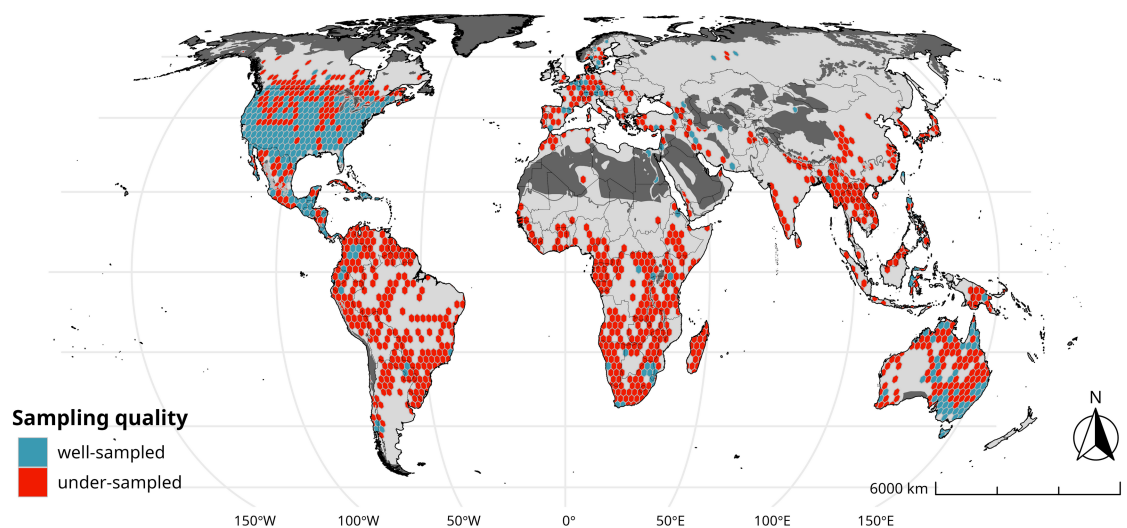


Figure 3. Sampling quality of amphibians at a global scale. Dark gray areas indicate regions excluded because no amphibian species distributions are expected there according to the (IUCN, 2024c) spatial data. Light gray represents the geographic extent of this work where completeness could not be estimated, and are thus classified as data-gap. Datum: Eckert IV projection, EPSG:54012.

Overlap with NPAs

The overlap of well-sampled with natural protected areas (NPAs), ranged from 11% to 32%, with the highest percentages observed in the Neotropic (32.47%), Afrotropic (28.38%) and Palearctic (25.47%) realms. For under-sampled areas, the overlap ranged from 10% to 29%, with the highest percentages in the Neotropic (29.41%), Afrotropic (25.24%), and Palearctic (20.47%) realms. For data-gap areas, the overlap ranged from 6% to 33%, with the highest percentages in the Neotropic (33.28%), Australasia (27.19%) and Afrotropic (18.06%) realms (Table 3).

Table 3. Overlap between well-sampled, under-sampled, and data-gap areas for amphibian distribution across realms and the natural protected areas. Areas expressed in million hectares (Mha). NPA percentages represent the proportion of NPAs area within each realm relative to the realm's total area, multiplied by 100. Category percentages reflect the overlap of each sampling category with NPAs, calculated by dividing the overlap area by the total area of that category within each realm and multiplying by 100. *ws*: well-sampled, *Us*: under-sampled, *Dg*: data-gap.

Realm	Total area	NPAs – area (%)	ws area	Us area	Dg area	Overlap with natural protected areas (NPAs)		
						ws – area (%)	Us – area (%)	Dg – area (%)
Afrotropic	2164.56	461.82 (21.34)	53.92	909.59	1201.05	15.3 (28.38)	229.58 (25.24)	216.94 (18.06)
Australasia	904.95	196.24 (21.69)	188.27	381.87	334.81	44.86 (23.83)	60.35 (15.8)	91.03 (27.19)
Indo-Malayan	848.39	72.81 (8.58)	12.36	325.04	510.99	1.63 (13.19)	39.44 (12.13)	31.74 (6.18)
Nearctic	1576.08	203.24 (12.9)	627.50	402.69	545.89	67.44 (10.75)	40.12 (9.96)	95.68 (17.52)
Neotropic	1887.44	591.83 (31.36)	128.72	909.03	849.69	41.79 (32.47)	267.33 (29.41)	282.71 (33.28)
Palearctic	3809.94	495.8 (13.01)	81.07	379.70	3349.17	20.65 (25.47)	77.74 (20.47)	397.41 (11.87)

Overlap with KBAs

The Neotropical, Afrotropical, and Indo-Malayan realms showed the highest overlap across all categories, with well-sampled areas ranging from 4% to 27% (highest in

Neotropical, 26.93%), under-sampled areas from 4% to 16% (highest in Neotropical, 15.58%), and data-gap areas from 3% to 13% (highest in Neotropical, 12.68%). The Palearctic realm also ranked high in the under-sampled category (15.07%) (Table 4).

Table 4. Overlap between well-sampled, under-sampled, and data-gap areas for amphibian distribution across realms and the key biodiversity areas. Areas expressed in million hectares (Mha). KBA percentages represent the proportion of KBAs area within each realm relative to the realm's total area, multiplied by 100. Category percentages reflect the overlap of each sampling category with KBAs, calculated by dividing the overlap area by the total area of that category within each realm and multiplying by 100. *ws*: well-sampled, *Us*: under-sampled, *Dg*: data-gap.

Realm	Total area	KBAs – area (%)	ws area	Us area	Dg area	Overlap with key biodiversity areas (KBAs)		
						ws – area (%)	Us – area (%)	Dg – area (%)
Afrotropic	2164.56	250.48 (11.57)	53.92	909.59	1201.05	12.67 (23.5)	121.34 (13.34)	116.47 (9.7)
Australasia	904.95	65.72 (7.26)	188.27	381.87	334.81	24.78 (13.16)	23.22 (6.08)	17.72 (5.29)
Indo-Malayan	848.39	90.31 (10.64)	12.36	325.04	510.99	2.4 (19.42)	43.28 (13.32)	44.63 (8.73)
Nearctic	1576.08	55.8 (3.54)	627.50	402.69	545.89	23.46 (3.74)	16.23 (4.03)	16.11 (2.95)
Neotropic	1887.44	284.01 (15.05)	128.72	909.03	849.69	34.67 (26.93)	141.62 (15.58)	107.72 (12.68)
Palearctic	3809.94	335.57 (8.81)	81.07	379.70	3349.17	11.4 (14.06)	57.22 (15.07)	266.95 (7.97)

Discussion

Our results indicate that amphibian sampling quality at the global level is geographically biased, and that greater efforts are needed to inventory amphibians in regions with the highest reported species richness.. The Nearctic and Australasia realms had the highest proportion of well-sampled areas, while the Neotropical, Indo-Malayan, and Afrotropical realms had the highest proportion of under-sampled areas. Data-gap areas were larger in the Palearctic, Indo-Malayan, and Afrotropical realms

(*question i*). Overall, the spatial congruence of all areas (i.e., well-sampled, under-sampled, and data-gap) with the NPAs was low, not exceeding 35% in any realm (*question ii*). Similarly, overlap with the KBAs was generally low, with well-sampled areas showing the highest overlap values, and only the Neotropic realm slightly exceeding 25% (*question 2*).

Our results are based on the distribution data for 93.6% of families (73 out of 78), 89.5% of genera (509 out of 569), and 56.2% of species (4891 out of 8708) of amphibians worldwide (Frost, 2024; Liedtke, 2019). Although our representativeness is relatively low compared to other ecological studies with amphibians worldwide, such as Mi et al. (2023) with 5403 species and Holt et al. (2013) with 6110 species, this might be due to our decision to exclusively use data from individuals deposited in museums and reported in GBIF. By making this decision, we aimed to reduce the overestimation of species distribution (species co-omission) related to the use of distribution polygons, such as those from the IUCN (Boitani et al., 2011), and to avoid potential identification bias by not including citizen science data deposited in GBIF (Girardello et al., 2019). Nevertheless, our study includes more than 55% of species for almost all families across all realms worldwide, and, in terms of absolute percentage, our representativeness is only 7.4% lower than that of other recent global studies on amphibians (i.e., Mi et al. 2023). Therefore, we consider our dataset to be representative enough to help to understand amphibian distributions gaps globally.

We detected a general disparity between the number of records for each realm. The Nearctic, Neotropical, and Australasian realms together accounted for the majority of records, comprising 86.8% of the total. This observation partially agrees with the results of Hughes et al. (2021), who found that the Nearctic, Australasia and Western

Europe were the best represented regions in terms of records number. Martin et al. (2012) mapped 2573 terrestrial study areas for work in ecology and found similar patterns, with most of study areas found in the Nearctic, Western Europe, Neotropic, Southeastern Australia and Oceania. In our study, the lowest number of records was for the Palearctic realm, comprising approximately 2.7% of the total records. Martin et al. (2012) and Hughes et al. (2021) both note a high concentration of records for different taxonomic groups and study sites in Western Europe. In contrast, except for Japan, records in Asia and Eastern Europe are relatively low. This pattern is evident in our record distribution map (Figure 1). Authors such as Beck et al. (2014) and Ivanova and Shashkov (2021) have reported geographical biases in GBIF records, suggesting that these biases may be related to the unequal distribution of research resources among countries, limiting their contributions to the databases GBIF relies on. When comparing data from the World Bank on "Research and Development" investment, it is evident that within the Palearctic realm, countries with higher GDP investments correspond to areas with more records (i.e., Western Europe, the Scandinavian Peninsula, Turkey, China, and Japan) (World Bank Open Data, 2024). Interestingly, the World Bank data also show that the Afrotropical, Indo-Malayan, and Neotropical realms have even lower GDP investments in Research and Development than several Palearctic countries, which would suggest a lower contribution in the number of records. However, Hughes et al. (2021) found a relationship between high-record points for different taxonomic groups and maritime and road routes, indicating that realms such as the Nearctic influence the number of records in the Neotropical region, while Western Europe and the Australasian realm influence the Afrotropical and Indo-Malayan realms. The high number of records in the Neotropical realm may be attributable to its high amphibian

species richness, considered the realm with a greater potential for new species descriptions and a continuous rate of new species description (Frost, 2024; Moura and Jetz, 2021; Vera Candioti et al., 2023). Consequently, the record density in this realm may be a reflect to its high species number.

The Nearctic and Australasian realms had the lowest percentages of data-gap areas and the highest proportions of well-sampled and under-sampled areas. In the other realms, the percentages of data-gap areas was greater than the combined percentage of well-sampled and under-sampled areas. Our observations on sampling completeness levels between realms are similar to those found by Girardello et al. (2019) for butterflies, who observed the same completeness patterns, being North America, Australia and Western Europe the regions with the highest butterfly sampling completeness, while South America, Africa and Eastern Europe-Asia had the lowest levels of completeness, similar to our findings. The differences in sampling completeness levels between realms may be related to the previously reported bias in the locations where ecological studies are conducted (Boakes et al., 2010; Martin et al., 2012; Romo et al., 2006). Realms such as the Nearctic, Australasian, and the western portion of the Palearctic have a higher number of recurrent ecological study sites, where biodiversity inventories can be more consistent, leading to higher sampling completeness. In contrast, realms like the Neotropical, Nearctic, Indo-Malayan, and the eastern portion of the Palearctic have a relatively low number of recurrent study sites (Beck et al., 2013; Boakes et al., 2010; Martin et al., 2012), and factors such as social and security instability (Hanson, 2018; Murillo-Sandoval et al., 2021; Siddig, 2019) limit the expansion of research areas. This contributes to increased knowledge gaps in the

distribution of various biological groups, such as amphibians, and consequently to gaps in completeness of biological inventories.

An interesting inverse pattern is observed between sampling completeness and species richness. The Neotropical, Afrotropical, and Indo-Malayan realms showed the highest number of species (Table 1). These realms, along with the Palearctic, exhibited the highest proportions of data-gap and under-sampled areas (Table 2, Figure 2). Distorted maps (area cartograms) based on sampling completeness and species richness (Figure 4) better illustrate this pattern. Moura and Jetz (2021), and Button and Borzée (2024), highlighted that most of the potential for discovering new vertebrate species lies in the Neotropical, Indo-Malayan, and Afrotropical realms. Similarly, Vera Candioti et al. (2023) emphasized the gaps in ecological and natural history knowledge of the larval stages of anurans (the most numerous group of amphibians), especially in the Neotropical and Indo-Malayan realms. Thus, the largest information gaps in distribution, natural history, and ecology occur precisely in the regions with the highest number of species. Given the transformation of ecosystems and global change affecting highly sensitive groups such as amphibians (Corn, 2005), and considering that completeness can also be interpreted as the probability of adding new species with continued sampling (Button and Borzée, 2024; Yang et al., 2013), it is possible that if research efforts are not increased in the under-sampled and data-gap areas of these realms, we may face the loss of species we have yet to discover.

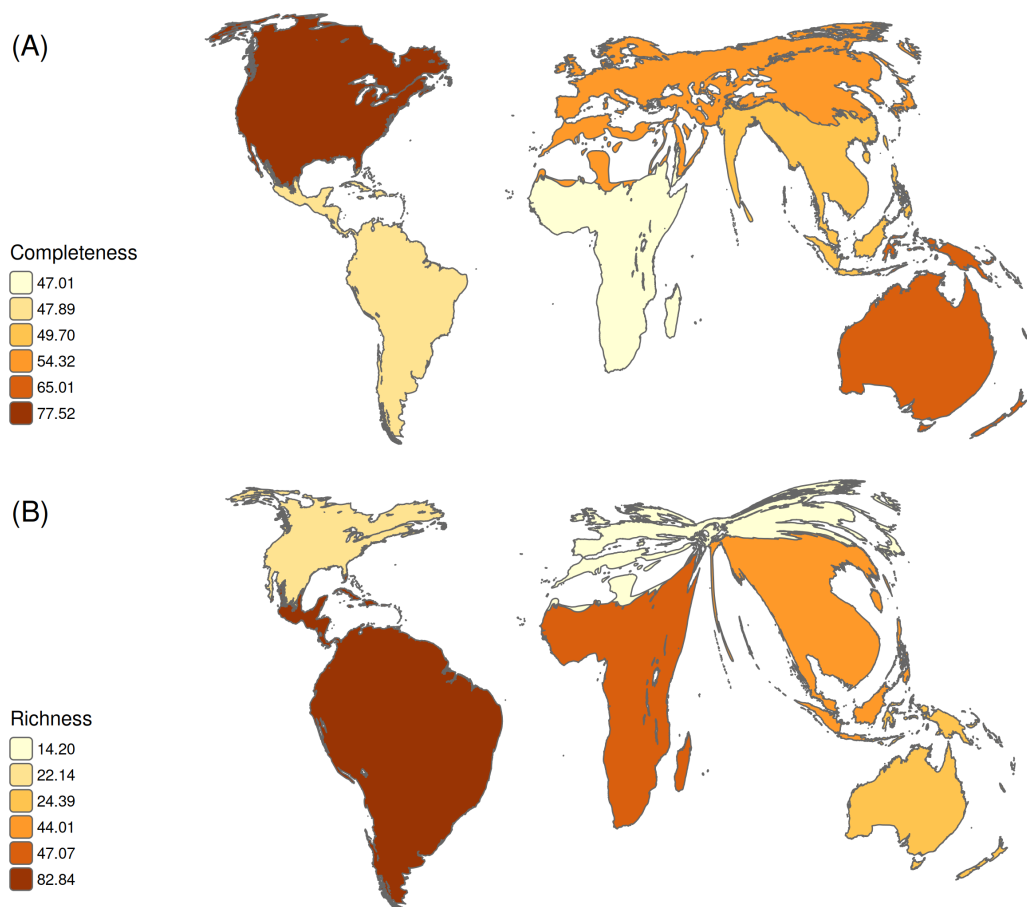


Figure 4. Area cartograms showing **A.** mean of sampling completeness per hexagon and **B.** mean of amphibian species richness per hexagon in each biogeographic realms. Larger polygons and warmer colors represent higher mean values per hexagon of sampling completeness or species richness in the realm.

The spatial overlap between well-sampled, under-sampled, and data-gap areas with Natural Protected Areas (NPAs) remained relatively low across biogeographic realms, staying below 35% (Table 3). Mi et al. (2023) noted that a significant proportion of amphibian species inhabit NPAs. Our results expand on this, suggesting that, while many amphibians occur in NPAs, the limited overlap with well-sampled areas points to gaps in understanding the full amphibian diversity within these protected regions. Campbell Grant et al. (2023) emphasize the need to determine the number and identity

of amphibian species within NPAs, so we could underscore the importance of targeting sampling efforts in these areas as a critical first step in conservation planning. Furthermore, substantial under-sampled and data-gap areas outside NPAs indicates the potential for populations of conservation-priority species or species yet to be described and should not be overlooked.

The spatial congruence between well-sampled and under-sampled areas with Key Biodiversity Areas (KBAs) was relatively low (less than 35%). KBAs are identified based on diverse multitaxonomic criteria to prioritize conservation areas, aiming for complementarity among sites (IUCN, 2016). These KBAs align with recent goals of the Kunming-Montreal Global Biodiversity Framework (KMGBF) established in 2022 (Kunming-Montreal Global Biodiversity Framework, 2022), which emphasizes conserving at least 30% of terrestrial and marine areas. KBAs should thus serve as the primary tool for defining new conservation areas based on biological criteria (IUCN, 2016; Plumptre et al., 2024). The alignment of well-sampled areas was proportionally higher than that of under-sampled and data-gap areas across all realms (Table 4), suggesting that KBAs primarily include areas where amphibian distributions are well-documented. However, the low overlap indicates that not all well-sampled areas are recognized as key conservation areas. Therefore, potential new KBAs may be supported by carefully examining under-sampled and data-gap areas. It is crucial to assess whether these regions support amphibian species and communities of significant biological and distributional importance, deserving inclusion in KBAs.

One of our objectives was to map areas with gaps in amphibian distribution data (undersampled and data-gap areas) and provide spatial information on where to prioritize sampling efforts. In Supplementary Information 2, we conduct a detailed

review of undersampled and data-gap regions at the biome level for each realm. However, as shown in Figure 3, it is critical to enhance sampling in the Neotropical, Indo-Malayan, and Afrotropical realms, which encompass the highest amphibian species richness and the largest undersampled and data-gap areas. These realms align with priority areas for the discovery of new vertebrate species as identified by (Moura and Jetz, 2021), and the Afrotropical and Indo-Malayan realms have had the fewest biological sampling stations established (Martin et al., 2012).

Recently, Button and Borzée (2024) used amphibians and their level of sampling completeness to underscore the importance of defining priority areas for the discovery of new vertebrates, taking into account sampling completeness. In this straightforward exercise, they found patterns similar to those presented in our work. However, unlike their study, ours reviews how these levels of completeness are globally distributed and the level of congruence between well-sampled, under-sampled, and data-gap areas with NPAs and KBAs. To our knowledge, our work is the first to attempt to quantify the sufficiency of sampling and the quality of amphibian distribution data on a global scale, utilizing data from accessible and open databases.

It is also important to emphasize the limitations of our study. Due to the taxonomic and geographic scale at which it was conducted, local applications may be challenging. The conservation by biome approach, presented in Supplementary Material 2, should help enhance the applicability of our findings on a local scale, by focusing on under-sampled or data-gap biomes within each domain rather than increasing sampling across entire hexagons. While GBIF offers a theoretically better alternative with fewer co-omission errors compared to occurrence data from other sources, it is still imperfect. In using these data, we applied curation steps to reduce potential biases and used a

completeness estimation method designed to mitigate bias from unequal sampling and heterogeneous data sources. However, due to our limited access to specimens and the fact that this falls beyond the scope of our study, we must rely on the proper identification of specimens deposited in museums. Additionally, given the scale used in the hexagons, we may have underestimated areas with information gaps. We hope this work serves as a starting point for directing research efforts both within and outside NPAs and KBAs, contributing to a better understanding of amphibian distribution based on specimen records at a global scale. We also anticipate that these data will improve KBAs and guide the development of new NPAs in line with international conservation goals.

Our study underscores that, for amphibians, much of the distribution information we have is incomplete, with larger gaps in some realms than in others. Given the challenges biodiversity faces from global change and human actions, rapid responses to understand species distribution and amphibian community structure are crucial. Only by understanding these aspects we should be able to devise effective conservation plans that align with political actions and global conservation initiatives, such as establishing natural protected areas and delineating key biodiversity areas. To quote Edward O. Wilson: “Biodiversity research requires more boots on the ground.” (Wilson, 2017). Based on our findings, amphibian sampling efforts should particularly focus on the Indo-Malayan, Afrotropical, and Neotropical realms, as well as the Asian portion of the Palearctic. These areas exhibit lower sampling completeness compared to other realms and have the potential to yield additional species for existing inventories.

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Funding

JMHL was funded with a doctoral scholarship (No. 88887.814811/2023-00) by Coordenação de Aperfeiçoamento de Pessoal de nível Superior (CAPES). MS acknowledges a research scholarship (MS: 309365/2019-8) by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Conflict of interest statement

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

Conceptualization: Jorge Mario Herrera-Lopera, Mirco Solé, Carlos Cultid-Medina; Methodology: Jorge Mario Herrera-Lopera, Mirco Solé, Carlos Cultid-Medina; Formal analysis and investigation: Jorge Mario Herrera-Lopera, Mirco Solé, Carlos Cultid-Medina; Writing - original draft preparation: Jorge Mario Herrera-Lopera; Writing - review and editing: Jorge Mario Herrera-Lopera, Mirco Solé, Carlos Cultid-Medina. All authors read and approved the final manuscript.

Data availability statement

The databases and R language code used for the analysis of this work are available in DRYAD at <http://datadryad.org/stash/share/N-QvzsruL2I9oEJPyriBVJWwFJWe2U4a82kklxKnok> or contacting the authors. To get processed spatial files please contact the authors.

Supplementary information

Mapping the missing: assessing amphibian sampling completeness and overlap with global protected areas

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Supplementary Information 1:

Selecting biogeographical proposal

We considered two biogeographical frameworks: Olson et al. (2001) modified by Dinerstein et al. (2017), and the framework proposed by Holt et al. (2013). To assess the suitability of these frameworks for amphibian distribution data, we took two approaches: (i) we created clusters using the Jaccard dissimilarity index (Carvalho et al. 2013) with a dissimilarity cutoff of 0.75, such that if two realms in a framework had a dissimilarity less than 0.75, we would deem it unsuitable; and (ii) using 2° wide hexagons as subsamples for each realm, we conducted an ANOSIM to determine if the variation within realms of each framework was smaller or greater than the variation between realms. If the variation between realms was smaller than the variation within realms, we would consider the framework unsuitable for our data.

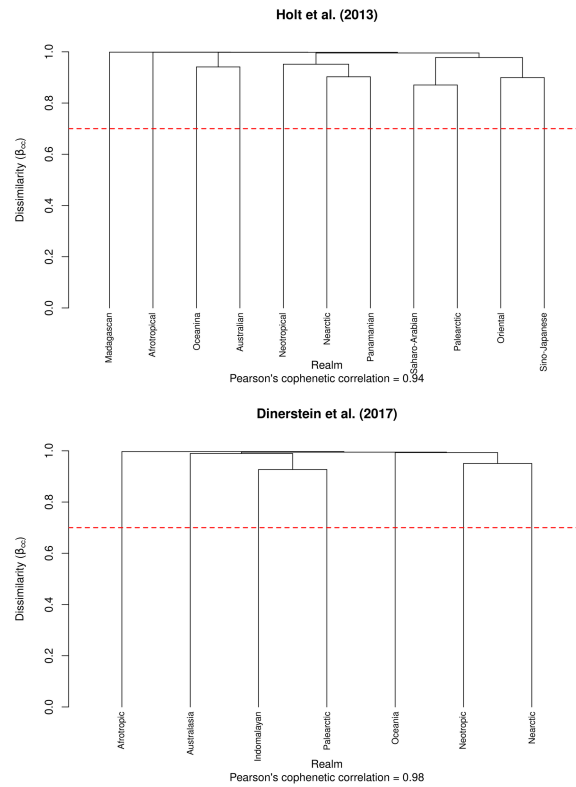


Figure S1. Clustering of realms according to Holt et al. (2013) and Dinerstein et al. (2017). Distance is measured using the Jaccard dissimilarity index. The line represents a dissimilarity cutoff of 75% (0.75).

For the first approach, we found that both Holt et al. (2013) realms and Dinerstein et al. (2017) realms may be suitable for separating amphibian distribution data at a global level (Figure S1). Therefore, based on the clustering results, either approach would be equally valid.

For the second approach, we found $R = 0.84$, $P < 0.00$ for Holt et al. (2013), and $R = 0.65$, $P < 0.00$ for Dinerstein et al. (2017). Positive values in the R statistic indicate greater variation between realms than within them, suggesting both biogeographical frameworks are suitable for analyzing global amphibian distribution, as per ANOSIM results.

Given both frameworks seemed equally valid for segmenting global amphibian distribution, we opted for Dinerstein et al. (2017) approach because it allows for the

analysis of information gaps at the biome level. Although a biome-level analysis is not one of our primary objectives, we included it as an additional analysis in Supplementary Information 2

Supplementary Information 2:

Well-sampled, under-sampled, and data-gap areas across biomes and realms

Afrotropic realm

Well-sampled areas: 2% of Afrotropical realm were well-sampled. These areas were located mainly in the southern and central-western regions, particularly in South Africa, and in smaller areas in Botswana, Namibia, Tanzania, Democratic Republic of Congo, Uganda and Ethiopia. The biomes with well-sampled hexagons were: Tropical & Subtropical Grasslands, Savannas & Shrublands, Mediterranean Forests, Woodlands & Scrub, Deserts & Xeric Shrublands and in smaller quantities Tropical & Subtropical Moist Broadleaf Forests and Montane Grasslands & Shrublands. The other biomes did not have any areas that could be classified as well sampled within this realm (Figure S2).

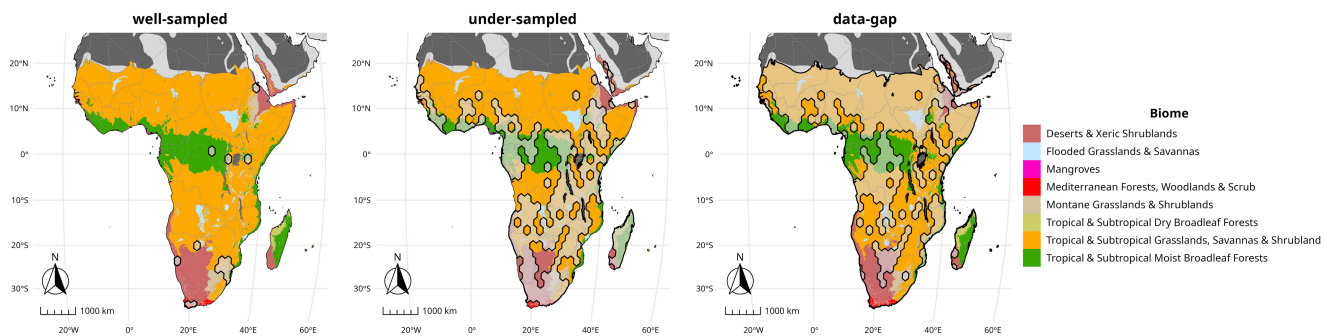


Figure S2. Well-sampled, under-sampled and data-gap areas in the biomes of Afrotropic realm. Dark gray areas indicate regions excluded because no amphibian species distributions are expected there according to the (IUCN 2024) spatial data. Light gray areas indicate the area belonging to other realms.

Under-sampled areas: 42% of the Afrotropical realm is under-sampled. These areas are primarily located in the southern, west-central, and east-central regions. Under-sampled areas exist in every country within the realm, except for Mauritania, Mali, and Chad. Most of Madagascar and the part of the realm within the Arabian Peninsula are also under-sampled. In terms of biomes, most under-sampled areas are found within the Tropical & Subtropical Grasslands, Savannas & Shrublands, Deserts & Xeric Shrublands, Tropical & Subtropical Dry Broadleaf Forests, and Tropical & Subtropical Moist Broadleaf Forests biomes. To a lesser extent, under-sampled areas are also present in the Mediterranean Forests, Woodlands & Scrub, Flooded Grasslands & Savannas and Montane Grasslands & Shrublands biomes (Figure S2).

Data-gap areas: 55% of the Afrotropical realm lacked sufficient data to estimate sampling completeness (i.e., had deficient-data). These deficient-data areas were mainly located in the northern and central regions of the realm and were present in every country within it. At the biome level, all except Tropical & Subtropical Dry Broadleaf Forests and Mediterranean Forests, Woodlands & Scrub had large areas with deficient-data. Notably, the Mangroves and Flooded Grasslands & Savannas biomes had the majority of their area with deficient-data. Additionally, the Tropical & Subtropical Grasslands, Savannas & Shrublands and Tropical & Subtropical Moist Broadleaf Forests biomes had extensive areas with deficient-data (Figure S2).

Australasia realm

Well-sampled areas: 21% of the Australasian realm was found to be well-sampled for amphibian distribution. The majority of these well-sampled areas were in Australia, with smaller portions in Papua New Guinea and Indonesia. In Australia, most well-sampled

zones were in the southeast, Tasmania, north, and central regions, with fewer well-sampled areas in the southeast and south-central regions. At biome level, the Temperate Broadleaf & Mixed Forests, Tropical & Subtropical Grasslands, Savannas & Shrublands, and Mediterranean Forests, Woodlands & Scrub biomes were well-sampled. To a lesser extent, the Temperate Grasslands, Savannas & Shrublands, Tropical & Subtropical Moist Broadleaf Forests, and Deserts & Xeric Shrublands biomes were also well-sampled. Nearly all well-sampled biomes were within Australia. In Papua New Guinea and Indonesia, portions of the Montane Grasslands & Shrublands and Tropical & Subtropical Moist Broadleaf Forests biomes were also well-sampled (Figure S3).

Under-sampled areas: 42% of the Australasian realm was found to be under-sampled. Most of these under-sampled areas were located in Papua New Guinea, Indonesia, and the northern, east-central, and southwestern regions of Australia. In terms of biomes, the Temperate Grasslands, Savannas & Shrublands, Tropical & Subtropical Grasslands, Savannas & Shrublands, Tropical & Subtropical Moist Broadleaf Forests, and Mediterranean Forests, Woodlands & Scrub biomes had the highest proportion of under-sampled areas (Figure S3).

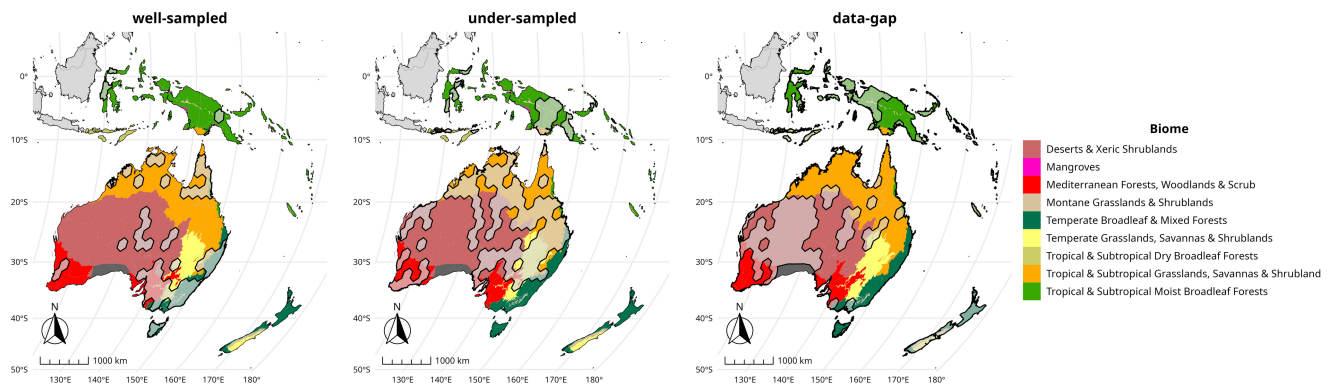


Figure S3. Well-sampled, under-sampled and data-gap areas in the biomes of Australasian realm.

Dark gray areas indicate regions excluded because no amphibian species distributions are expected there according to the (IUCN 2024) spatial data. Light gray areas indicate the area belonging to other realms.

Data-gap areas: The Australasian realm had 37% of its area categorized as deficient-data. Most of these areas were located in New Zealand, Indonesia, and the western and central regions of Australia. In terms of biomes, the Tropical & Subtropical Dry Broadleaf Forests, Mangroves, Tropical & Subtropical Moist Broadleaf Forests, Montane Grasslands & Shrublands, and Deserts & Xeric Shrublands had the largest proportion of their areas classified as deficient-data (Figure S3).

Indo-Malayan realm

Well-sampled areas: Well-sampled areas accounted for 1% of the total area of the Indo-malayan realm. These areas were located in Taiwan, the Philippines, and Myanmar, covering small portions of the Tropical & Subtropical Moist Broadleaf Forests and Tropical & Subtropical Dry Broadleaf Forests biomes (Figure S4).

Under-sampled areas: Under-sampled areas accounted for 38% of the Indo-malayan realm. The majority of this area was found in the Indochinese Peninsula and the western portion of India. Additionally, other under-sampled areas were identified in Malaysia, Indonesia, Sri Lanka, China, and the Philippines. In terms of biomes, most of the under-sampled areas were located in the Tropical & Subtropical Moist Broadleaf Forests, Tropical & Subtropical Dry Broadleaf Forests, and Tropical & Subtropical Grasslands, Savannas & Shrublands (Figure S4).

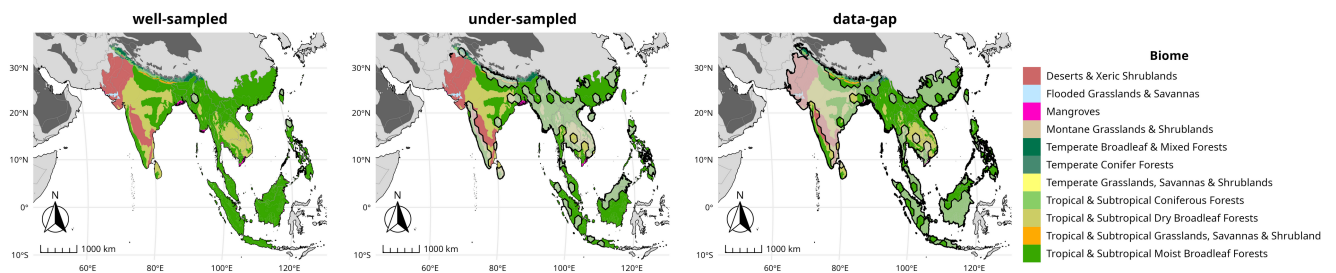


Figure S4. Well-sampled, under-sampled and data-gap areas in the biomes of Indo-malayan realm.

Dark gray areas indicate regions excluded because no amphibian species distributions are expected there according to the (IUCN 2024) spatial data. Light gray areas indicate the area belonging to other realms.

Data-gap areas: Deficient-data areas covered 60% of the Indo-malayan realm. These areas were predominantly located in the Indian subcontinent, China, Indonesia, and Thailand. All biomes had areas with deficient-data. However, the Mangroves, Flooded Grasslands & Savannas, and Tropical & Subtropical Dry Broadleaf Forests biomes

stand out, with the majority of their area within the realm classified as data-gap areas (Figure S4).

Neartic realm

Well-sampled areas: Well-sampled areas comprised 40% of the entire Neartic realm. The majority of these areas were located in the United States, with smaller portions in Mexico and Canada. Significant portions of all biomes were classified as well-sampled, although the Boreal Forests/Taiga and Tropical & Subtropical Coniferous Forests biomes had comparatively smaller proportions (Figure S5).

Under-sampled areas: Under-sampled areas comprised 26% of the total area of the Neartic realm. These areas were predominantly located in the central-northern regions of the United States, southern Canada, and northern Mexico. The majority of under-sampled areas were concentrated in the Temperate Broadleaf & Mixed Forests, Temperate Grasslands, Savannas & Shrublands, and Deserts & Xeric Shrublands biomes (Figure S5).

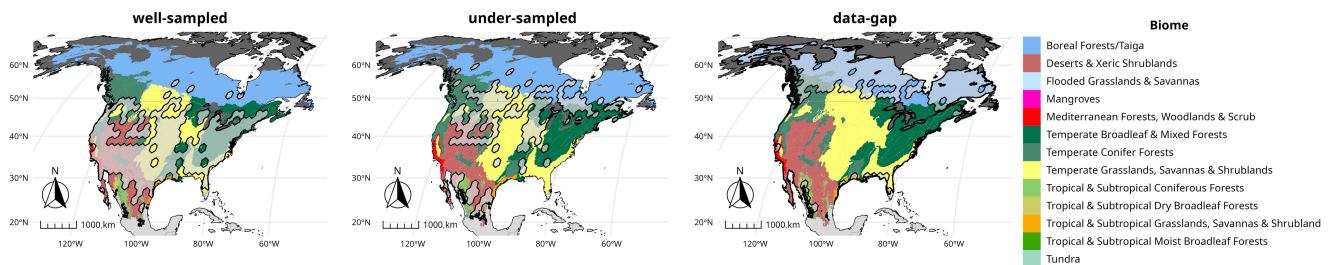


Figure S5. Well-sampled, under-sampled and data-gap areas in the biomes of Neartic realm. Dark gray areas indicate regions excluded because no amphibian species distributions are expected there according to the (IUCN 2024) spatial data. Light gray areas indicate the area belonging to other realms.

Data-gap areas: Data-gap areas accounted for 35% of the Nearctic realm. These areas were mainly distributed in Canada, the southern United States, and the western portion of northern Mexico. Regarding biomes, nearly all data-gap areas were concentrated in the Tropical & Subtropical Coniferous Forests, Temperate Broadleaf & Mixed Forests, Tropical & Subtropical Moist Broadleaf Forests, as well as Temperate Grasslands, Savannas & Shrublands, and to a lesser extent, Tropical & Subtropical Grasslands, Savannas & Shrublands (Figure S5).

Neotropic realm

Well-sampled areas: Well-sampled areas covered 7% of the total area of the Neotropical realm. These areas were located in the Andean region, specifically in the northern Andes and the southern portion between Argentina and Chile, as well as in

southeastern Brazil, and in Central America, including Guatemala, Belize, Costa Rica, and Panama. At the biome level, most well-sampled areas were in the Tropical & Subtropical Moist Broadleaf Forests, Tropical & Subtropical Grasslands, Savannas & Shrublands, and Tropical & Subtropical Dry Broadleaf Forests. There were smaller proportions in Mangroves and Temperate Broadleaf & Mixed Forests (Figure S6).

Under-sampled areas: Under-sampled areas covered 48% of the total Neotropical realm. These areas were present in all countries within the realm except El Salvador and Guatemala. Furthermore, under-sampled areas were found in all biomes within the realm, with smaller proportions in the Tropical & Subtropical Dry Broadleaf Forests, Temperate Grasslands, Savannas & Shrublands, and Montane Grasslands & Shrublands biomes (Figure S6).

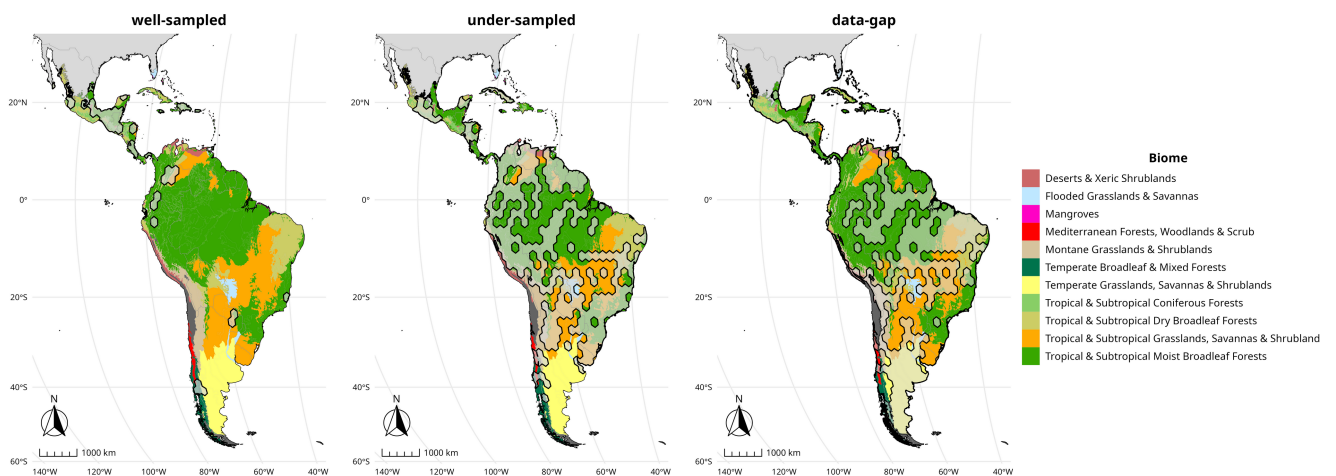


Figure S6. Well-sampled, under-sampled and data-gap areas in the biomes of Neotropical realm. Dark gray areas indicate regions excluded because no amphibian species distributions are expected there according to the (IUCN 2024) spatial data. Light gray areas indicate the area belonging to other realms.

Data-gap areas: Data-gap areas covered 45% of the total area of the Neotropical realm. The majority of these areas were located in South America, with some exceptions in Mexico and the Caribbean. In South America, data-gap areas were especially prevalent in the Amazon region, and in northern, northeastern, and western Brazil, as well as in Argentina. Most data-gap areas were found in the Tropical & Subtropical Moist Broadleaf Forests, Temperate Grasslands, Savannas & Shrublands, and Montane Grasslands & Shrublands biomes. To a lesser extent, they were also present in the Tropical & Subtropical Grasslands, Savannas & Shrublands, Tropical & Subtropical Dry Broadleaf Forests, and Deserts & Xeric Shrublands biomes (Figure S6).

Palearctic realm

Well-sampled areas: Well-sampled areas comprised 2% of the Palearctic realm. These areas were primarily located in the central-western region of Europe, the Scandinavian and Iberian Peninsulas, and Central Asia. Additionally, there were scattered well-sampled spots in the Balkans region and North Africa, particularly between Egypt and Israel. At the biome level, most well-sampled areas were found in the Temperate Broadleaf & Mixed Forests and Mediterranean Forests, Woodlands & Scrub biomes, with smaller proportions in the Deserts & Xeric Shrublands and Temperate Grasslands, Savannas & Shrublands biomes (Figure S7).

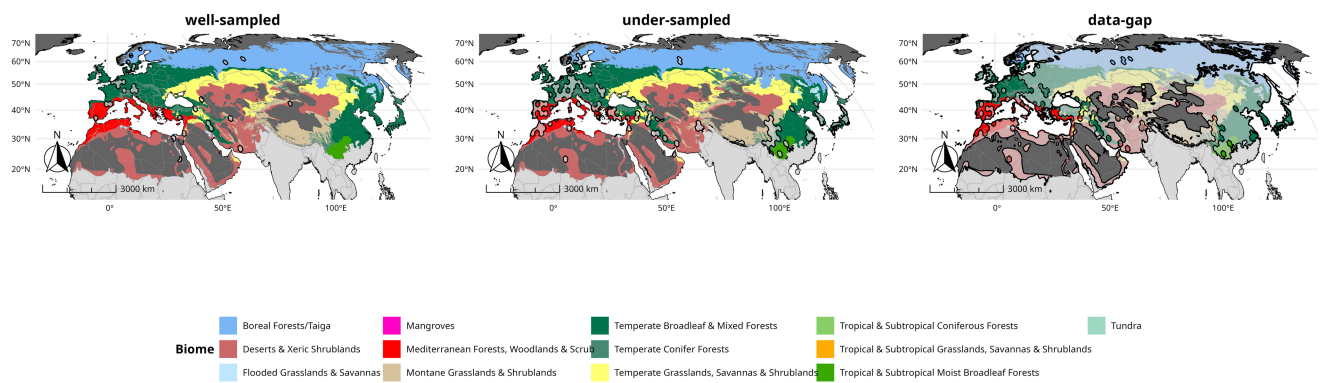


Figure S7. Well-sampled, under-sampled and data-gap areas in the biomes of Palearctic realm. Dark gray areas indicate regions excluded because no amphibian species distributions are expected there according to the (IUCN 2024) spatial data. Light gray areas indicate the area belonging to other realms.

Under-sampled areas: Under-sampled areas accounted for 10% of the total area of the Palearctic realm. These areas were primarily distributed in Western Europe, particularly in the Iberian Peninsula, the Mediterranean region, and the Scandinavian Peninsula. Under-sampled areas were also found in the western part of Asia, China, the Korean Peninsula, and Japan. At the biome level, the main under-sampled areas were in the Mediterranean Forests, Woodlands & Scrub, Montane Grasslands & Shrublands, and Temperate Broadleaf & Mixed Forests biomes, with smaller proportions in the Temperate Grasslands, Savannas & Shrublands, and Boreal Forests/Taiga biomes (Figure S7).

Data-gap areas: Data-gap areas covered 88% of the total area of the realm. Consequently, these areas spanned nearly the entire realm, with the exception of Western Europe and East Asia (the Korean Peninsula, Japan, and China). Given their extensive distribution, data-gap areas were present in all biomes, with smaller

proportions found in the Temperate Broadleaf & Mixed Forests and Mediterranean Forests, Woodlands & Scrub biomes (Figure S7).

Supplementary Information 3:

Choosing hexagon size

To select the hexagon size (resolution) within the analysis, (i) we calculated the effect size of the hexagon on species richness and sampling completeness using omega squared (ω^2) as the effect size measure (Kroes and Finley 2023), chosen for its low sensitivity to sample size differences and violation of the equal variances assumption. Additionally, (ii) we compared the 95% confidence intervals for species richness and sampling completeness across hexagon sizes. For both approaches, hexagon sizes ranged from 1° to 3.5°, with increments of 0.5°.

In terms of effect size, we determined that both species richness and completeness were influenced by hexagon size to a degree of less than 1% (ω^2 richness: 0.007, ω^2 completeness: 0.002). Thus, objectively, the hexagon size used exerts minimal influence on sampling completeness and species richness. In terms of comparing confidence intervals for species richness and sampling completeness across different hexagon sizes, we observed an increasing trend in both metrics as hexagon size increases (Figure S8), consistent with findings from other studies (Bosco et al. 2022; Victorero et al. 2023). It's important to note that increasing hexagon size also increases errors of co-omission, where species presence is assumed within an area lacking confirming evidence. Hexagon sizes of 2° show significantly higher values of richness and completeness compared to 1° and 1.5° hexagons, with completeness values statistically equivalent to those of hexagons up to 3°, making it a potentially suitable middle ground. Moreover, this resolution aligns with the used by Holt et al. (2013). Given these considerations and the effect size being less than 1%, we opted for

a 2° hexagon size to optimize richness and completeness while mitigating the risk of excessive co-omission errors.

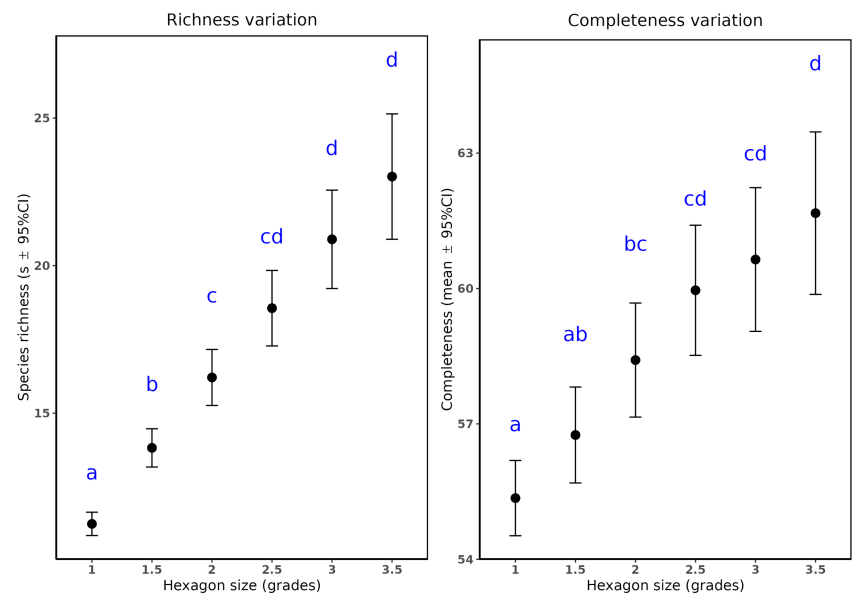


Figure S8. Variations in A. Species richness and B. Sampling completeness using different resolutions (hexagon sizes). Bars indicate 95% confidence intervals.

Supplementary Information 4:

Sampling completeness and completeness slope.

Completeness (Figure S9A) and accumulation curve slope (Figure S9B) observed at the global level. The accumulation curve slope was used as the basis for classifying well-sampled and under-sampled areas. Following a modified approach based on the criteria of Yang et al. 2013 and Girardello et al. 2019, we defined three categories: (i) “well-sampled” (slope ≤ 0.05), (ii) “under-sampled” (slope > 0.05), and (iii) “data-gap,” referring to areas where species records are expected according to (IUCN 2024) spatial data but where sampling completeness could not be assessed due to insufficient records (i.e., record-to-species ratio ≤ 1).

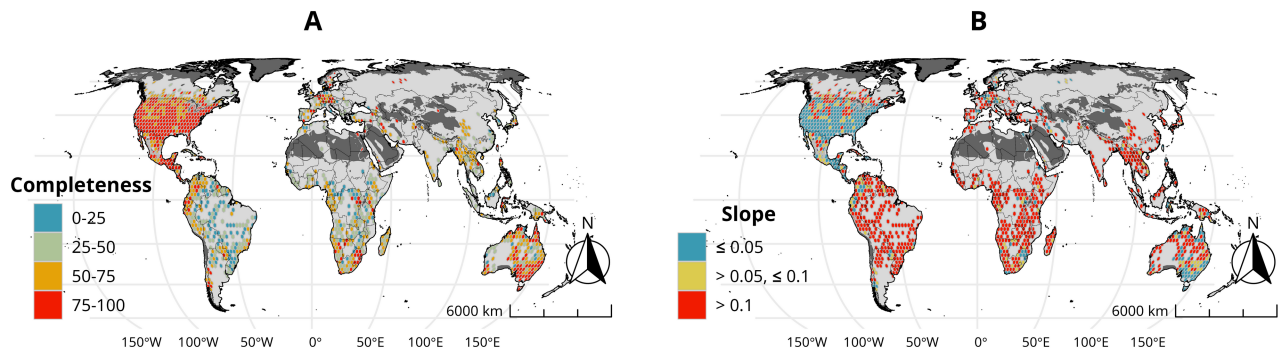


Figure S9. A. Sampling completeness estimation, B. Accumulation curve slope

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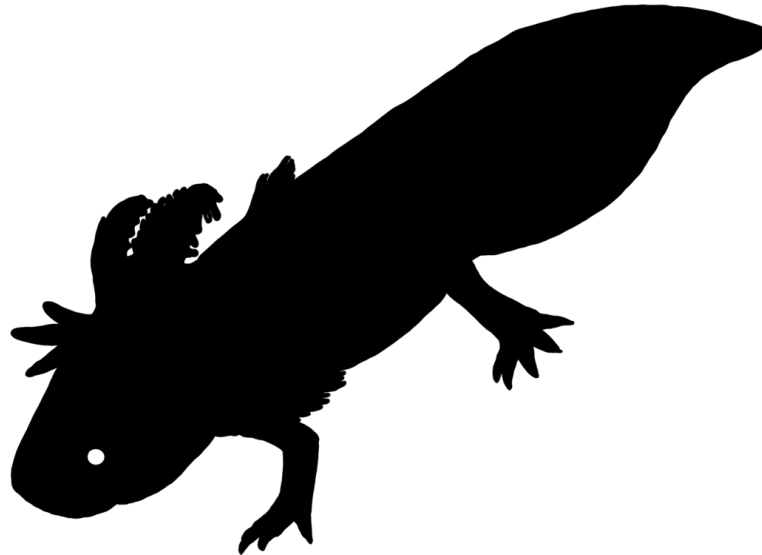
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Capítulo 2

We need to protect Amphibians... but where? A global assessment of Priority Areas based on Multidimensional Diversity

Artigo submetido a Diversity and distributions - ISSN: 1472-4642



Ambystoma mexicanum - Chuanxin Yu

PhyloPic CC BY 4.0

“Grandma, what happens to Darwin’s frogs when they go away? Will they come back? Or will they live with Sharptooth [= Tyrannosaurus rex] and unicorns?”

I had just read my book The Mystery of Darwin’s Frog to Fionna. She was fascinated by the papa frog brooding tadpoles in his vocal sac, but she was particularly curious— and concerned— about the frogs disappearing from Chile. How does one explain to a three-year-old that extinction is forever?

A three-year-old who firmly believes that T. rex still lives somewhere, and that unicorns really exist, just not in her world.

I began, “We have to protect the forests where Darwin’s frogs live. If all the Darwin’s frogs die, they will be gone forever. There’s no way to get them back.””.

“Vovó, o que acontece com os sapos de Darwin quando eles vão embora? Eles voltam? Ou vão viver com o Tiranossauro Rex e os unicórnios?”

Eu tinha acabado de ler meu livro O Mistério do Sapo de Darwin para Fionna. Ela ficou fascinada com o sapo papai cuidando dos girinos em sua bolsa vocal, mas ficou particularmente curiosa — e preocupada — com o desaparecimento dos sapos do Chile. Como explicar para uma criança de três anos que a extinção é para sempre?

Uma criança de três anos que acredita firmemente que o T. rex ainda vive em algum lugar e que os unicórnios realmente existem, só que não no mundo dela.

Comecei: “Temos que proteger as florestas onde vivem os sapos de Darwin. Se todos os sapos de Darwin morrerem, eles desaparecerão para sempre. Não há como recuperá-los.””.

Marty Crump

**We need to protect Amphibians... but where? A global assessment of Priority
Areas based on Multidimensional Diversity**

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Acknowledgments

We gratefully acknowledge the taxonomists, ecologists, naturalists, and other professionals from a wide range of disciplines for their efforts in collecting, curating,

and sharing open-access biological data, without which this work, and so many others, would not be possible.

Abstract

Amphibians are the most threatened vertebrate group, with habitat loss as the leading driver of their decline. Their extinction implies more than the loss of species, but loss of key ecosystem functions and lineages. Therefore, identifying priority areas for amphibian conservation must go beyond traditional metrics focused only on species richness or threat status. Here, we present a global assessment of priority areas for amphibian conservation based on multidimensional diversity, integrating taxonomic, functional, and phylogenetic alpha and beta diversity. Using over 5,300 species and predictive models calibrated across six biogeographic realms, we identified spatial patterns of amphibian diversity and classified each region into conservation priority categories. Our results reveal that the highest priority areas do not consistently align with species richness hotspots, highlighting the importance of incorporating multiple biodiversity dimensions. Although some of the identified Very High Priority (VHP) areas overlap with existing Protected Areas (PAs) and Key Biodiversity Areas (KBAs), the congruence is variable (~ 8% to ~ 50%) and often limited—especially in the Nearctic, Indo-Malayan, and Palearctic realms. These mismatches underscore gaps in current conservation frameworks and the need to refine spatial planning strategies. Our findings offer a reproducible analytic protocol for identifying conservation priorities that can be adapted to finer spatial scales (e.g., country, state, locality, etc.). By aligning multidimensional biodiversity with conservation targets set by the Kunming-Montreal Global Biodiversity Framework, this approach can guide more inclusive and ecologically meaningful conservation actions.

Key words

Alpha and beta diversity, Conservation gaps, Global Biodiversity Framework, Key Biodiversity Areas, Protected Areas, Spatial conservation planning

1. Introduction

Modern Protected Areas (PAs), originally established as landscape preserves and game reserves in North America and Europe, and as zones to safeguard forest remnants in the Americas, Asia, and Africa (Chape et al. 2008) have emerged as the most effective strategy for conserving biodiversity *in situ* (Watson et al. 2014, 2016). These areas not only protect a wide array of species but also preserve critical ecosystem services, including regulation, provisioning, and cultural functions (Watson et al. 2016; Schirpke et al. 2021). Complementing PAs, the Key Biodiversity Areas (KBAs) initiative by the International Union for Conservation of Nature (IUCN) identifies sites of exceptional biological value, whether for their unique species, ecosystems, or the presence of populations of threatened species (KBA Standards and Appeals Committee of IUCN SSC and IUCN WCPA 2022). However, PA designations are frequently shaped by the imperative to meet international commitments, often resulting in the protection of areas that are suboptimal for biodiversity conservation, typically lands with low conflict with competing uses like agriculture or urban expansion (Venter et al. 2018). Even when biological factors are considered, the focus tends to be on threatened species or species richness (Margules and Pressey 2000; Rodrigues et al. 2004), neglecting other critical realms of biodiversity, such as ecological functions and evolutionary lineages. The same issue is observed in KBAs, whose criteria disproportionately emphasize the presence of threatened species and ecosystems (KBA Standards and Appeals Committee of IUCN SSC and IUCN WCPA 2022).

Although protecting threatened species is a central goal of conservation, emblematic cases such as the Iberian lynx and the California condor and its parasites reveal a critical limitation of single-species approaches: they may inadvertently cause the extinction of associated, less visible species, along with their unique evolutionary

histories and ecological functions (Pérez et al. 2013; Rózsa and Vas 2015). Furthermore, although threatened species may play important roles within ecosystems, there is no consistent evidence indicating that they are functionally more relevant than non-threatened species (González-del-Pliego et al. 2024). On the other hand, relying only on species richness provides an incomplete picture of biodiversity, as it overlooks evolutionary lineage and functional roles within ecosystems. Therefore, several authors advocate for a multidimensional perspective in designing PAs, one that integrates not only taxonomic diversity, but also functional diversity (i.e., the range of services species provide) and phylogenetic diversity (i.e., the evolutionary relationships among them), while assessing how unique these trait combinations are in a given regional context (Margules and Pressey 2000; Leenhardt et al. 2015; Socolar et al. 2016; Gumbs et al. 2021).

The Kunming-Montreal Global Biodiversity Framework, under its Target 3, calls for the effective conservation of at least 30 per cent of terrestrial and inland water areas, and of marine and coastal areas, especially areas of particular importance for biodiversity and ecosystem functions and services, by 2030 (Kunming-Montreal Global Biodiversity Framework 2022). This global commitment, adopted by the majority of nations, plays a central role in shaping today's international conservation agenda. Notably, the target emphasizes “biodiversity”, a term that, as defined by (Solbrig 1991), refers to “the property of groups of living entities to be varied,” encompassing a wide range of biological entities including genes, cells, individuals, species, communities, and ecosystems (Solbrig 1991; Vellend 2016). This variation may occur along different dimensions: in the case of communities, for example, it may reflect species identities (taxonomic diversity), ecological roles (functional diversity), or evolutionary histories

(phylogenetic diversity) (Begon et al. 2006; Magurran and McGill 2011; Chao et al. 2021). In this broader sense, the most biodiverse areas are those that not only host high levels of species, functions, and lineages (i.e., areas of high multidimensional diversity), but also sustain compositional turnover of these dimensions across space (Melo et al. 2009; Sonne and Rahbek 2024). Consequently, adopting multidimensional diversity as a guiding criterion for the designation of protected areas could offer a robust alternative to current approaches focused primarily on species richness or the presence of threatened species, aligning more closely with global conservation targets. Amphibians are the most threatened group of vertebrates worldwide, with around 41% of species classified under some threat category (IUCN SSC Amphibian Specialist Group 2024). Habitat loss remains the leading cause behind their population declines (Luedtke et al. 2023). Although (Mi et al. 2023) found that most amphibian species occur within PAs, this does not necessarily mean their populations are adequately safeguarded. We also lack a clear understanding of how well amphibian diversity is protected in terms of functional traits and evolutionary lineages. Given the significant global data gaps for amphibians (Herrera-Lopera et al. 2025), and the likelihood that the environmental conditions they depend on will deteriorate in the coming years (Alves-Ferreira et al. 2025), identifying global priority areas to conserve their multidimensional diversity is a critical and urgent task.

This study aimed to identify global priority areas for amphibian conservation by integrating alpha and beta taxonomic, functional, and phylogenetic diversity. We also quantified the proportion of these priority areas currently covered by existing Protected Areas (PAs) and Key Biodiversity Areas (KBAs), in order to identify critical conservation gaps. Our findings provide valuable insights to inform the strategic expansion of PAs

and KBAs, contributing to the achievement of global conservation targets outlined in the Kunming-Montreal Global Biodiversity Framework. Our results also help to understand how strategies such as Protected Areas and Key Biodiversity Areas can be strategies that help us to conserve regions with the highest amphibian biodiversity, and how using species richness as the main metric for conservation area designation and nomination may lead to the loss of biological information within the broad definition of biodiversity.

2. Materials and methods

2.1 Biogeographic regionalization and geographic extent

We adopted the biogeographic regionalization proposed by Olson et al. (2001) and later refined by Dinerstein et al. (2017) to delineate our study's biogeographic extent and contextualize our results within each realm. This framework divides the world into eight biogeographic realms: Afrotropic, Antarctic, Australasia, Indo-Malay, Nearctic, Neotropic, Oceania, and Palearctic.

Antarctic and Oceania were excluded from our analysis: Antarctic due to the natural absence of amphibians, and Oceania because amphibians are largely absent from most oceanic islands (Duellman and Trueb 1994; Vitt and Caldwell 2014). Furthermore, records from Oceania represented only about 0.03% of the total dataset (75 records).

We further constrained our study's geographic extent using IUCN-provided spatial data for species distributions (IUCN 2024), ensuring that diversity estimations were not generated for areas where species are unlikely to occur. While some records from the databases used in this study fell outside the extent defined by IUCN polygons,

we consider the integration of IUCN polygons as an extent filter to be a robust approach for delineating amphibian distributions on a global scale.

For each realm, we partitioned the area into hexagonal polygons (e.i., minimal analysis unit) of 2 degree width (~222.64 km at the equator) (Fig. 1). Compared to squares, hexagons provide a more accurate representation of distances and areas while also enhancing the visual clarity of spatial patterns (Birch et al. 2007). We generated the hexagonal polygons using functions from the R packages *sf*, *terra*, and *tidyterra* (Pebesma 2018; Hernangómez 2023; Hijmans 2024; R Core Team 2024).

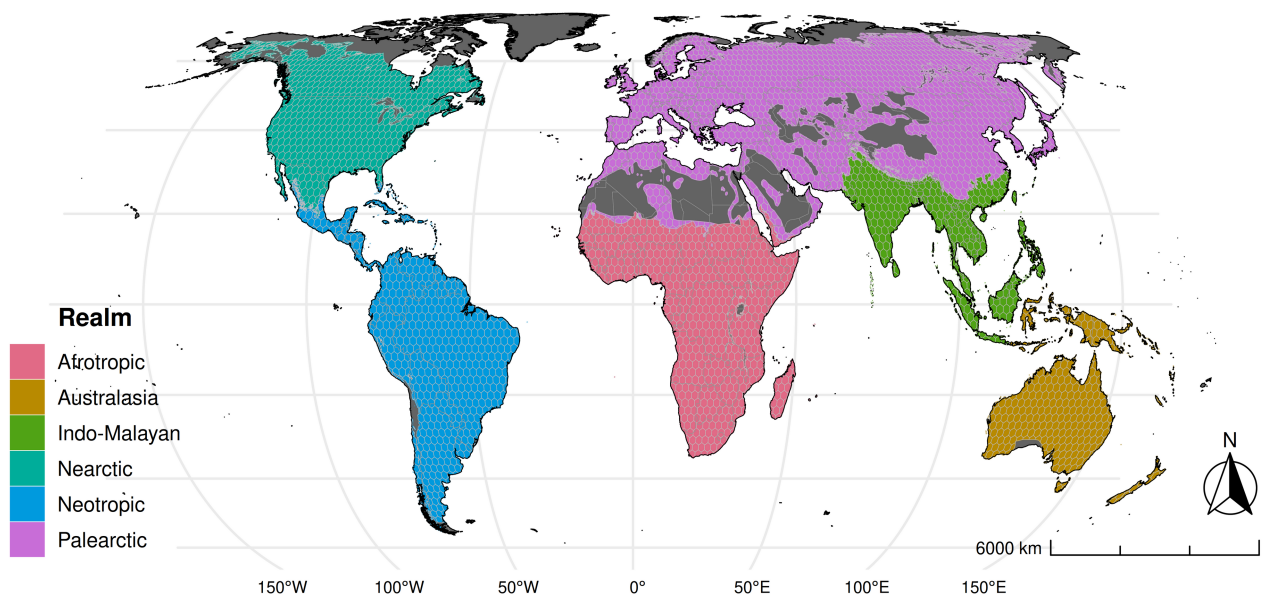


Figure 1. Extent of study. Each unit represents a biogeographic realm as defined by Dinerstein et al. (2017). Dark gray areas indicate excluded regions, as they are unlikely to host amphibian species according to spatial data from the IUCN (2024). Projection: Eckert IV, ESRI:54012.

2.2 Species records

Species records were obtained from GBIF, considering only georeferenced records with museum support to minimize possible misidentifications (search DOI: GBIF.Org, 2024). Records were curated using functions from the *scrubr* and *CoordinateCleaner* R packages (Zizka et al. 2019; Chamberlain 2022) to filter erroneous coordinates, museum locations, and marine records. Only unique species-coordinate combinations were retained for diversity analyses. Taxonomic updates and corrections were performed using the *AmphiNom* R package (Liedtke 2019), based on the *Amphibian Species of the World 6.2* database from the American Museum of Natural History (Frost 2024). Taxonomic information is current as of April 2024. After data cleaning and taxonomic updates, our database comprised 5,350 amphibian species across 523 genera and 72 families. Both the database and the code used for record cleaning and analysis are available in the data availability section.

We excluded areas without amphibian distribution data according to the IUCN spatial data (IUCN, 2024) to avoid including records and predicting distribution in regions where amphibians are not expected to occur. While some GBIF records fall within these excluded regions, aligning our analysis with the expert-informed IUCN distribution polygons provides a standardized approach.

2.3. Functional traits

Functional traits were obtained from Moura et al. (2024) and Oliveira et al. (2017). The traits included in our analysis were: activity pattern (diurnal, nocturnal, or both), habitat use (terrestrial, arboreal, aquatic, fossorial, or any combination), body size (snout-vent length), body mass, and reproductive strategy (direct development, larval

stage, or viviparity). These traits were selected for their relevance in capturing different aspects of species' interactions with their ecosystems (González et al. 2016).

Continuous traits (body size and mass) were categorized into four groups based on quartiles, considering all species in the study area. This transformation ensured comparability across species while minimizing noise from continuous data variation. Furthermore, given that amphibian body size and mass may vary among populations (e.g., Rebouças et al., 2018), we consider that categorizing these traits provides a more reliable representation of each species' relative traits in comparison to others. Missing trait values were imputed using the mean or most frequent value within the species' genus (Gunton et al. 2011; Fried et al. 2012). While some studies suggest this approach is not the most robust (Taugourdeau et al. 2014), the large dataset and limited natural history information on species with missing data prevented the use of more refined methods, such as ecological or phylogenetic imputations (Taugourdeau et al. 2014; Moura et al. 2024).

2.4 Species phylogenetic position

The phylogenetic tree used in our analyses was obtained from *TimeTree 5* (Kumar et al. 2022), an online platform that compiles phylogenetic data from various published studies across multiple taxonomic groups. For amphibians, the most recent tree (until October 2024) includes 4,284 species. Taxonomic updates of tree were performed using the *AmphiNom* package in R (Liedtke 2019). Missing species in phylogeny were incorporated as sister groups (polytomies) within their respective genera, or family in case of monotypic genera (Fritz and Rahbek 2012). Species placement within the phylogeny was carried out using the *V.Phylomaker* package in R (Jin and Qian 2019, 2022).

2.5 Environmental and Climatic Variables

For the predictive models (see the data analysis section), we used 20 environmental and climatic variables from CHELSA version 2.1 (chelsa-climate.org, Karger et al., 2021a). Including temperature- and precipitation-derived bioclimatic variables (Bio1–Bio19), as well net primary productivity. CHELSA variables offer superior predictive power for species distribution models compared to those from other global databases (e.g., WorldClim, Bobrowski et al., 2021), provide more accurate predictions in topographically complex regions (Bobrowski and Udo 2017), and yield more precise estimations for precipitation-derived variables (Karger et al. 2021b). Additionally, we used elevation, latitude and longitude as predictive variables, we obtained and used the digital elevation model (DEM) from WorldClim (Fick and Hijmans 2017). A detailed list of the variables used in our analysis is presented in Supplementary Information 1.

CHELSA variables and WorldClim DEM have a resolution of 30 arc-seconds (~ 1 km at the equator). To match them with our response unit (the hexagons described in section 2.1), we averaged the values of the cells within each hexagon, generating a single value per hexagon (similar to procedure followed by Pavanetto et al., 2024).

2.6 Data analysis

2.6.1 Alpha and beta diversity measures

We estimated multidimensional alpha diversity (i.e., taxonomic, functional, and phylogenetic) for amphibians using Hill numbers (Hill 1973; Jost 2006; Chao 2024). Since our diversity estimations were based on GBIF occurrence data, which compile information from heterogeneous sources, we lacked unbiased abundance measures (Lobo 2008). Therefore, we focused on diversity estimations in order zero ($q = 0$), which

does not account for abundances in the estimations (Hill 1973; Jost 2006), and can be interpreted as species richness (${}^0\text{TD}$), functional group richness (${}^0\text{FD}$), or lineage richness (${}^0\text{PD}$), according to diversity dimension (Chao et al. 2021).

Because functional and phylogenetic diversity estimations (${}^q\text{FD}$ and ${}^p\text{D}$) require a "weight" for species within each hexagon (Hsieh et al. 2016; Chao 2024), we generated incidence matrices by subdividing each hexagon into sub-hexagons of 0.2 width-degrees (~22 km at the equator). These incidence matrices can be used as a substitute for abundance matrices in diversity estimation (Chao et al. 2021). While this procedure may introduce biases in abundance-based estimations due to the heterogeneous sources of GBIF occurrence data, by using only order-zero measures ($q = 0$), which do not consider abundances or frequencies in incidences, we ensured that this procedure remains purely operational and does not affect the diversity estimations used in our work. Diversity estimations were performed using the *iNEXT.3D* package in R (Chao and Hu 2025).

To estimate the multidimensional beta diversity (i.e., taxonomic, functional, and phylogenetic) of amphibians in each realm, we used the approach by Cardoso et al., (2014b), which extends Jaccard-based beta partitioning (Carvalho et al. 2013) to include functional traits and phylogenetic positions. This yields three beta diversity metrics: taxonomic beta ($T\beta$, equivalent to Jaccard), functional beta ($F\beta$), and phylogenetic beta ($P\beta$), all insensitive to abundance, making them suitable for our study. We analyzed each realm separately, computing pairwise distance matrices for each diversity dimension. To capture overall beta diversity patterns (accounting for both turnover and richness differences), we used total beta diversity ($T\beta_{\text{total}}$, $F\beta_{\text{total}}$, and

$P\beta_{total}$) as our beta measure (Cardoso et al. 2014b). Beta calculations were performed using the *BAT* package in R (Cardoso et al. 2014a).

Because alpha and beta diversity estimations may be unreliable with small species and record numbers, we calculated alpha and beta diversity measures only for those hexagons that had at least three species and more than three records.

2.6.2. Multidimensional alpha and beta diversity models

Since the available global data on amphibians is geographically biased (Hughes et al. 2021; Herrera-Lopera et al. 2025), it was necessary to use predictive models to estimate amphibian diversity across the entire geographic extent. To achieve this, we fitted alpha and beta diversity models using environmental, geographic, and climatic variables. For both alpha and beta diversity models, we only considered, as data-input, data from hexagons with a Sampling Coverage (SC - Chao et al., 2014) greater than 0.5 to reduce the noise introduced by highly under-sampled hexagons.

Prior to modeling, we conducted a correlation analysis within each realm to mitigate collinearity, excluding variables with an absolute Spearman correlation coefficient above 0.7 (Quinn and Keough 2002; Zuur et al. 2009) using the *caret* package in R (Kuhn 2007).

For alpha diversity, we fitted generalized linear models (GLMs) for each diversity measure and for each realm separately, aiming to create models that best fit the specific context of each realm. We tested Poisson, Quasi-Poisson, and Negative Binomial distribution families for taxonomic diversity of order zero (0TD - species richness) and Gaussian, Gamma (link = "log"), and Inverse Gaussian (link = "log") distributions for functional and phylogenetic diversity of order zero (0FD - functional group richness and 0PD - lineage richness, respectively) (Buckley 2015). We then

selected the best-fitting distribution in each case using the corrected Akaike Information Criterion (AICc) (Zuur et al. 2009; Burnham and Anderson 2010). To validate models prior to comparison, we assessed variance inflation factors (VIF), removing variables exceeding a VIF of 10 in an iterative process (Zuur et al. 2009). Additionally, we checked model residuals for overdispersion, clustering patterns (heteroscedasticity/independence issues), and uniformity in simulated residuals (Zuur et al. 2009; Hartig 2016; Montgomery et al. 2020). We also applied Moran's test to detect spatial autocorrelation in our models residuals. Since our models are designed for prediction rather than inference, and because Moran's index never exceeded 0.4 (remaining below 0.3 in most cases), we opted to retain the GLMs. This choice was further justified by the fact that introducing spatial structures in Generalized least squares models (GLS) removed key relationships between variables, and spatially explicit models (SAR) are not recommended for predictive purposes (Zuur et al. 2009; Negrete-Yankelevich and Fox 2015). To ensure the validity of our models, we conducted an additional analysis comparing predicted and observed values to verify that predictions remained meaningful. For each realm, the predictive model for each variable was selected based on the lowest AICc after validation, without considering model complexity, as our focus was on predictive accuracy (Richards 2015). GLMs validation and selection were performed in R using functions from the *performance* and *MuMin* packages (Bartoń, Kamil 2010; Lüdecke et al. 2019). The final models chosen and the evaluation of deltas of model-predicted and observed values can be found in Supplementary Information 2.

To predict beta diversity between hexagon pairs, we used the compositional dissimilarity calculated in Section 2.6.1 and the absolute differences in environmental

variables between hexagons to train Random Forest models (Breiman 2001). These models, which rely on multiple regression trees, are well-suited for capturing complex variable relationships, as expected for beta diversity (Cutler et al. 2007). For model training and validation, we allocated 85% of the data for training and 15% for testing, generating trees 1,000 times using the randomForest package in R (Breiman et al. 2002). A separate Random Forest model was fitted for each variable within each realm to enhance specificity. Performance metrics (i.e., MSE, R^2 , and explained variance) of models used for predictions are summarized in Supplementary Information 3.

2.6.3. Model projection and classification of priority areas

Both the GLMs and Random Forest models were projected across the entire study area (extent). Since beta diversity is meaningful only when comparing pairs, and because comparing two very distant hexagons is not particularly relevant, (given that we expect diversity to vary spatially), we defined beta diversity for each hexagon as its average dissimilarity with adjacent hexagons (i.e., those sharing a border). This approach was similar to the procedure followed by Melo et al. (2009). Thus, the projected beta diversity of each hexagon reflects its dissimilarity within its surrounding neighborhood. For isolated hexagons without direct neighbors (such as small islands), we did not assign a beta diversity value to avoid overestimation when measuring beta diversity across distant hexagons.

We defined priority areas as hexagons exhibiting the highest multidimensional alpha and beta diversity (taxonomic, functional, and phylogenetic) within each realm. To combine these measures, we standardized them (scale between 0 - 1). We then determined the maximum diversity value for each dimension within each realm and calculated the difference (delta) between each hexagon's diversity and its realm's

maximum. The summed deltas were then used to derive an overall diversity score for each hexagon. Hexagons with the highest multidimensional diversity had the lowest delta values, meaning they were closest to the maximum diversity within their realm. This method follows a logic similar to that used in ternary plots (e.g., Pierce et al., 2017), but extended to six dimensions. Finally, each hexagon was classified into four priority level categories based on quantiles: "Very high" (VHP), for hexagons with the smallest difference from the realm's maximum diversity values, "High" (HP), "Medium" (MP), and "Low" (LP), with the latter including hexagons with the greatest difference from the realm's maximum diversity values. For isolated hexagons where no beta diversity value was assigned (due to a lack of adjacent hexagons), priority classification was based solely on alpha diversity values (about 68 of hexagons, 1.4% of total).

2.6.4. Overlap of Very High and High priority areas with Protected Areas and Key Biodiversity Areas

Protected Areas (PA) were sourced from The World Database on Protected Areas (WDPA - August 2023 version), the most comprehensive global database of terrestrial and marine PAs. It includes various conservation categories such as National Parks, Habitat Reserves, Indigenous Reserves, and Ramsar Areas. The polygon data are publicly available at *protectedplanet.net* (UNEP-WCMC and IUCN 2023). Key Biodiversity Areas (KBAs) were obtained upon request from *keybiodiversityareas.org* (BirdLife International 2024), we used March 2024 version.

To quantify the extent to which VHP/HP Areas are currently covered by existing PAs/KBAs, we calculated the percentage of spatial match (Nori et al. 2020). This was determined by measuring the shared area between each priority category and the PAs/KBAs, then dividing it by the total area of that priority category to estimate the

proportion of priority area overlapped with PAs or KBAs. The analysis was performed separately for each realm, using a global equal-area projection (Eckert IV, ESRI:54012) to ensure accurate spatial representation. All analyses were conducted in R, using the *terra* and *tidyterra* packages (Hernangómez 2023; Hijmans 2024).

3. Results

3.1. Multifunctional diversity of biogeographic realms

Alpha diversity patterns varied across realms. For alpha diversity, the Afrotropical and Palearctic realms exhibited higher phylogenetic diversity compared to their maximum values than functional and taxonomic diversity. In the Australasia, Nearctic, and Neotropic realms, functional and phylogenetic diversity showed similar relative values, both exceeding taxonomic diversity. In the Indo-Malayan realm, functional diversity was the highest, surpassing both phylogenetic and taxonomic diversity (Fig. 2A-B). For beta diversity, taxonomic dissimilarity was the highest across all realms except Australasia and Nearctic, where functional and phylogenetic dissimilarity, respectively, exhibited the highest relative values (Fig. 2C-D).

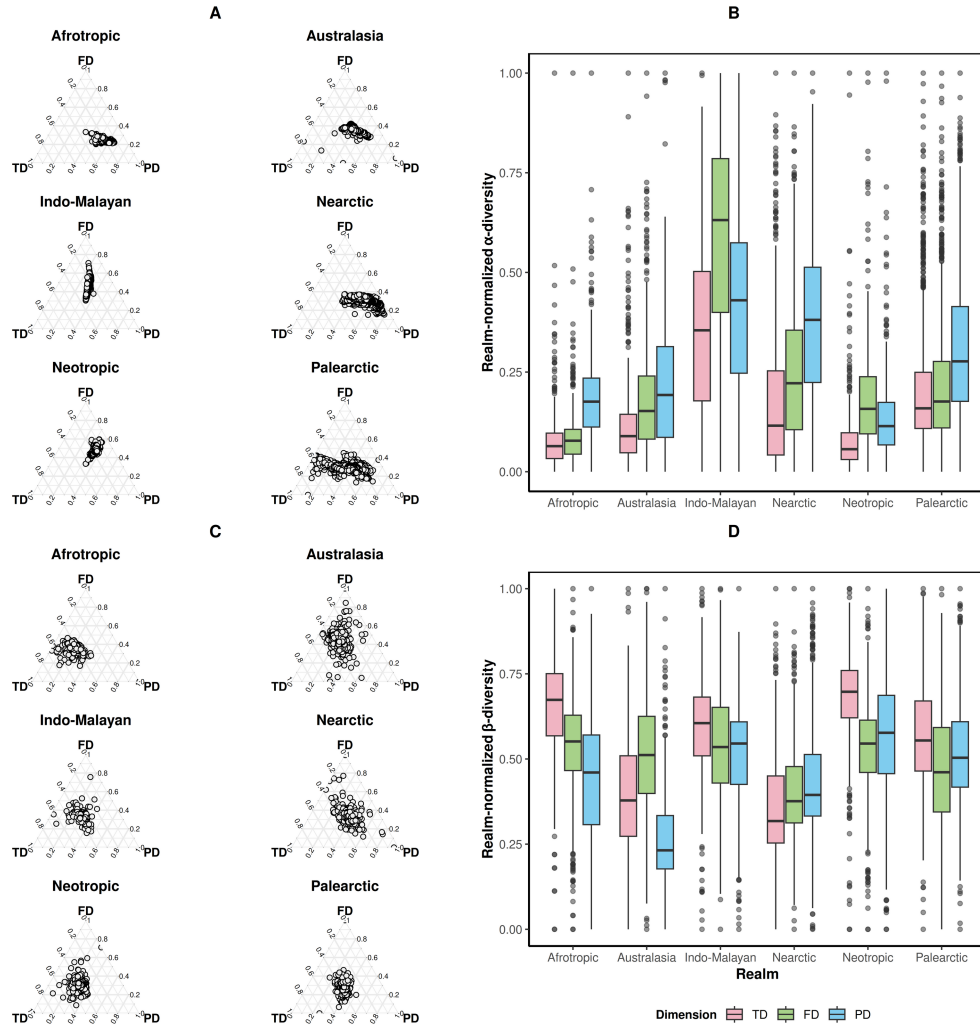


Figure 2. Normalized multidimensional alpha (A-B) and beta (C-D) diversity values for hexagons across biogeographic realms. Ternary plots (A, C) illustrate the relative contributions of taxonomic (TD), functional (FD), and phylogenetic (PD) diversity in each realm. Boxplots (B, D) show the distribution of normalized multidimensional diversity values per realm.

3.2. Priority Areas

Priority areas for amphibian conservation, identified based on high multidimensional alpha and beta diversity, are shown in Fig. 3. Because diversity values were normalized within each realm, comparisons between realms are not meaningful, and the results should be interpreted within each realm's context. VHP

areas tended to form clusters across different regions within each realm and were mostly connected by HP areas (Fig. 3).

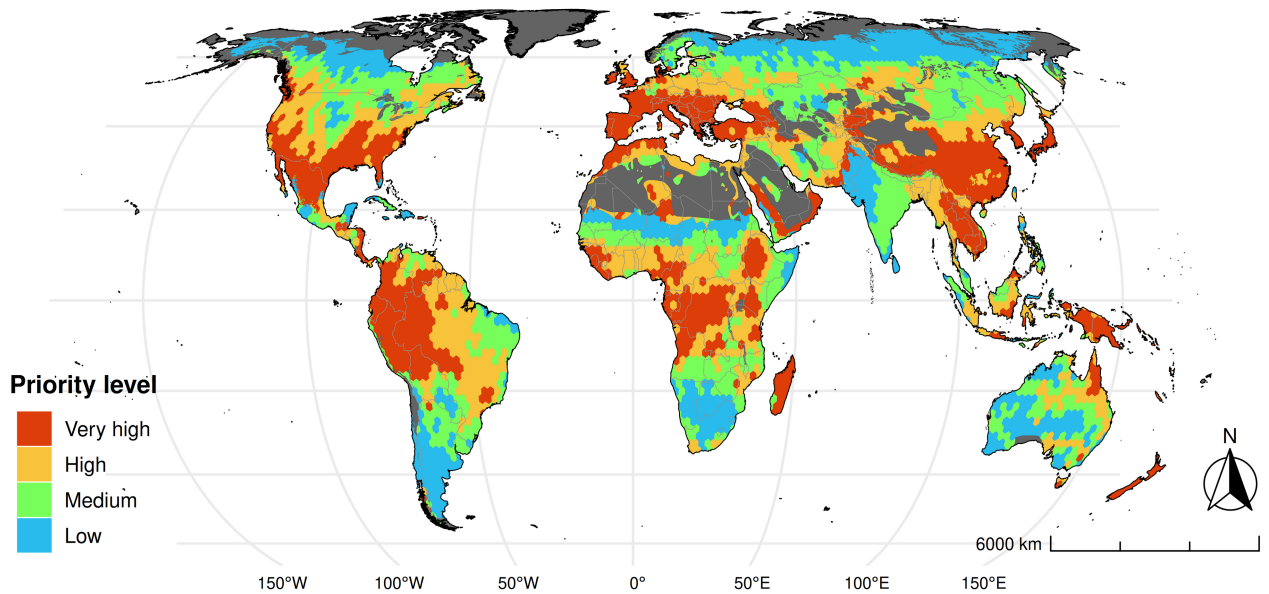


Figure 3. Global priority areas for amphibian conservation based on multidimensional alpha and beta diversity. Each realm is standardized relative to its own maximum values, so comparisons between realms are not meaningful, and interpretations should be made independently within each realm. Projection: Eckert IV, ESRI: 54012.

In the Afrotropical realm, the main VHP clusters were concentrated in Central Africa, with additional groupings in Eastern Africa (Ethiopia and Madagascar) and Western Africa (around Guinea, Sierra Leone, and Liberia). In Australasia, VHP clusters were primarily found in Polynesia (New Zealand), Melanesia (Papua New Guinea and the Solomon Islands), and across Australia, particularly in the northern (Queensland) and southern regions (New South Wales and Tasmania). In the Indo-Malayan realm, key VHP clusters were observed in Maritime Southeast Asia

(Indonesia and Borneo), Mainland Southeast Asia (Indochina Peninsula, including Laos, Cambodia, and Vietnam), and southern China. In the Nearctic realm, a major VHP cluster extended from the Mexican Transition Zone into the southern United States, forming a "V"-shaped pattern along both the Pacific and Atlantic coasts, reaching the U.S.-Canada border. In the Neotropical realm, VHP clusters were mainly found in the Northern Andes, the Amazon region, southern Central America (northern Panama and Costa Rica), and the Brazilian Atlantic Forest. Lastly, in the Palearctic realm, significant VHP clusters appeared in the Mediterranean region covering its Asian, European, and African portions and across the Sino-Japanese region, spanning both continental and island areas (Fig. 3).

3.3. Very High and High Priority Areas within PAs and KBAs

The overlap between VHP areas and PAs varied across biogeographic realms, ranging from 12.67% in the Indo-Malayan to 47.65% in the Neotropic. While, the proportion of PAs intersecting with VHP areas ranged from 16.36% in Australasia to 45.41% in the Neotropic realm. For HP areas, the overlap with PAs was lowest in the Indo-Malayan realm (10.31%) and highest in the Neotropic (33.61%). While, the proportion of PAs overlapping with HP areas varied from 16.83% in Australasia to 32.33% in the Afrotropic realm (Table 1).

Table 1. Spatial overlap between Very High Priority (VHP) and High Priority (HP) areas with Protected Areas (PAs) across biogeographic realms. Areas are reported in million hectares (Mha).

Realm	Area	PL	PL area	PAs area	Overlap area	PL overlap (%)	PAs overlap (%)
Afrotropic	2164.56	VHP	537.64	465.76	127.75	23.76	27.43
		HP	593.70		150.60	25.37	32.33
Australasia	904.95	VHP	140.74	200.95	32.88	23.36	16.36
		HP	212.36		33.83	15.93	16.83

Indo-Malayan	848.39	VHP	206.00	73.32	26.11	12.67	35.60
		HP	227.03		23.40	10.31	31.92
Nearctic	1576.08	VHP	437.52	215.32	68.78	15.72	31.94
		HP	466.62		52.54	11.26	24.40
Neotropic	1887.44	VHP	566.96	595.00	270.18	47.65	45.41
		HP	554.66		186.44	33.61	31.33
Palaearctic	3809.94	VHP	1066.52	529.68	197.94	18.56	37.37
		HP	1016.54		138.58	13.63	26.16

The overlap between VHP areas and KBAs varied from 6.50% in the Nearctic to 18.92% in the Neotropic. For HP areas, overlap ranged from 2.87% in the Nearctic to 15.09% in the Neotropic. In terms of KBAs, the proportion intersecting with VHP areas ranged from 21.72% in Australasia to 50.98% in the Nearctic, while for HP areas, it ranged from 24.04% in the Indo-Malayan realm to 32.78% in the Palaearctic (Table 2).

Table 2. Spatial overlap between Very High Priority (VHP) and High Priority (HP) areas with Key Biodiversity Areas (KBAs) across biogeographic realms. Areas are reported in million hectares (Mha).

Realm	Area	PL	PL area	KBAs area	Overlap area	PL overlap (%)	KBAs overlap (%)
Afrotropic	2164.56	VHP	537.64	250.45	82.50	15.35	32.94
		HP	593.70		67.11	11.30	26.79
Australasia	904.95	VHP	140.74	65.73	14.28	10.15	21.72
		HP	212.36		17.66	8.32	26.87
Indo-Malayan	848.39	VHP	206.00	89.82	22.43	10.89	24.97
		HP	227.03		32.59	14.35	36.28
Nearctic	1576.08	VHP	437.52	55.80	28.45	6.50	50.98
		HP	466.62		13.41	2.87	24.04
Neotropic	1887.44	VHP	566.96	283.98	107.25	18.92	37.77
		HP	554.66		83.71	15.09	29.48
Palaearctic	3809.94	VHP	1066.52	335.58	155.04	14.54	46.20
		HP	1016.54		109.99	10.82	32.78

4. Discussion

Prioritizing areas for the in situ conservation of biodiversity is one of the major challenges in the face of global change scenarios. This study offers spatially explicit data that can guide local-scale conservation efforts, contributing to the preservation of amphibian diversity worldwide. Our study also reveals that the relative contribution of different biodiversity dimensions varies across biogeographic realms, suggesting that conservation strategies based solely on species richness may overlook key aspects such as ecosystem function and evolutionary history. The priority categories we propose offer a valuable opportunity to strengthen ecological connectivity among Protected Areas and Key Biodiversity Areas, supporting international conservation targets while maximizing the protection of amphibian biodiversity.

4.1. Contributions of the diversity dimensions

Although it might be expected that, consistently across realms, hexagons with higher species richness (TD) would exhibit higher values of functional richness (FD) and phylogenetic richness (PD), our results show that this pattern is not consistent within the different realms. Within them, trends of higher relative contributions of certain diversity dimensions are observed, such that one realm may contain localities with values near the maximum in PD without this necessarily corresponding to high values in TD and/or FD. This uneven contribution of diversity dimensions within realms was more evident in alpha diversity measures than in beta diversity, but it is consistent with findings from other studies in other scales, that have assessed the relationships between diversity dimensions (e.g., Chen et al., 2023; E-Vojtkó et al., 2023; Hähn et al., 2024; Robroek et al., 2017) and have found that there is not necessarily an exact correspondence between different dimensions of diversity. Instead, they may be

decoupled at different spatial or temporal scales. This highlights the importance of considering the different dimensions of biological diversity when delimiting priority areas at a global level, given that there is no direct correspondence between diversity dimensions. Considering all of them is the most efficient way to ensure that prioritization accounts for the unique diversity variations across different realms.

4.2. Priority areas for amphibian conservation

The VHP areas for amphibian conservation identified in our study encompass both globally recognized biodiversity *hotspots* (Myers et al. 2000; Mittermeier et al. 2011; Bellard et al. 2014; Sonne and Rahbek 2024) and regions overlooked in broader-scale analyses, such as the North American Coastal Plain and southeastern China (Noss et al. 2015; Xu et al. 2024). Notably, our framework also identified critical areas absent from global *hotspot* assessments, including Central Africa and the Amazon region. Discrepancies between our prioritization and previous global *hotspot* identifications (e.g., Myers et al., 2000) stem from methodological differences. While conventional *hotspot* identification analyses typically rely on species richness, phylogenetic diversity, and/or endemism metrics, our approach incorporates a multidimensional biodiversity assessment (species, functional, and phylogenetic richness) and includes an analysis of contextual variation in relation to adjacent regions. This methodology captures broader biodiversity signals beyond simple species richness metrics, yielding a more comprehensive conservation prioritization strategy. Furthermore, our analysis was conducted independently for each biogeographic realm, enabling the identification of regionally significant conservation areas that might be undervalued in global-scale assessments yet serve as crucial refuges for exceptional concentrations or unique species, functional traits, or lineages

within their regional context. Additionally, our results provide evidence that VHP areas are interconnected through HP zones, as illustrated in Figure 3. This spatial arrangement highlights a significant opportunity for designing ecological corridors that link the most diverse amphibian regions within and across realms. Such connectivity is essential for effectively fulfilling the targets set by the KMGBF (Santini et al. 2016; Kunming-Montreal Global Biodiversity Framework 2022).

It is important to emphasize that the identification of priority areas for amphibian conservation presented here should not be interpreted as a rigid framework, but rather as a dynamic guide. Due to the categorical nature of our classification, approximately 25% of each realm's surface is designated as Very High Priority (VHP), 25% as High Priority (HP), 25% as Medium Priority (MP), and 25% as Low Priority (LP). In situations where VHP or HP zones are no longer viable for conservation—owing to urban development or established land-use commitments—MP zones may serve as realistic alternatives for protected area expansion. Given the spatial resolution of our analysis, our aim is primarily to provide a descriptive overview of global patterns of multidimensional amphibian diversity. Thus, our results are best suited to inform conservation decision-making at broad spatial scales and should be re-evaluated within the context of local land-use policies and the configuration of existing protected area networks. In this regard, our approach is conceptually aligned with previous efforts to delineate global conservation priorities (Myers et al. 2000; Sonne and Rahbek 2024), but stands out by incorporating multiple dimensions of biodiversity.

4.3. Overlap of Priority Areas with Protected Areas and Key Biodiversity Areas

Our findings reveal significant variation in the extent to which Very High Priority (VHP) and High Priority (HP) areas overlap with Protected Areas (PAs) and Key

Biodiversity Areas (KBAs) across biogeographic realms. The Neotropical realm exhibited the highest overlap, with almost half of VHP areas falling within PAs, followed by Australasia, where about a quarter of such areas are similarly protected. Conversely, the Nearctic, Indo-Malayan, and Palearctic realms showed much lower levels of overlap, generally under or around 18% of VHP areas located inside PAs. A comparable pattern was observed for HP areas, where the Neotropics showed over a third, while Afrotropics showed about a quarter overlap with PAs, while the Nearctic, Indo-Malayan, and Palearctic regions remained below 15%. These differences may be rooted in the distinct historical contexts and conservation rationales that guided the creation of PAs in each realm. In the Nearctic, for example, the earliest protected areas were often established to safeguard landscapes of scenic, economic, or recreational significance—paralleling Western European traditions that prioritized game reserves. In contrast, Neotropical PA systems were frequently designed to protect Indigenous lands, Pleistocene refugia, freshwater sources (which are especially critical for amphibians), watershed integrity, and to promote biodiversity-based tourism. This contrast illustrates how conservation priorities have shaped the types of areas selected for protection (see Chape et al., 2008). While contemporary PA systems across all realms now commonly aim to safeguard biodiversity and maintain ecosystem services such as water regulation and cultural heritage (Chape et al. 2008; Watson et al. 2014), the legacy of their founding motivations may still influence their spatial configuration. In the Indo-Malayan realm, where overlap values were among the lowest for both VHP and HP areas, data limitations may contribute to underrepresentation. The global protected area database acknowledges that many forms of local or community-based protection in this realm (and others) are either unrecognized or lack sufficient

documentation to be included in global assessments (Chape et al. 2008; Stevens 2014; ICCA Consortium 2021).

An additional factor that may help explain the observed spatial overlap between priority areas and PAs is the proportion of land under protection within each biogeographic realm. As expected, realms with a larger extent of protected land tend to exhibit higher overlap with biodiversity priority areas identified in our analysis. Based on values from Table 1, the percentage of land currently protected in each realm is as follows: Neotropical (31.52%), Australasian (22.20%), Afrotropical (21.52%), Palearctic (13.90%), Nearctic (13.66%), and Indo-Malayan (8.64%). Notably, the Neotropical, Australasian, and Afrotropical realms—those with the highest proportion of protected land—also showed the greatest spatial overlap between PAs and areas of very high or high priority. In contrast, the Indo-Malayan, Nearctic, and Palearctic realms, which have lower coverage of protected areas, exhibited the lowest levels of overlap. This pattern highlights the potential of our results to inform and strengthen PAs networks across biogeographic realms. In line with Target 3 of the Kunming-Montreal Global Biodiversity Framework—which calls for the protection of at least 30% of the planet’s terrestrial surface—our identified priority areas could guide the strategic expansion and improved connectivity of existing PAs. Such efforts would not only support the achievement of global biodiversity targets, but also enhance the long-term conservation of amphibian diversity across realms.

The overlap between Key Biodiversity Areas (KBAs) and areas of Very High Priority (VHP) or High Priority (HP) was generally low across all biogeographic realms, never exceeding 21%. The highest overlap was observed between VHP areas and KBAs in the Neotropical realm, reaching 20.6%. This limited congruence may be

explained by several factors. First, the total extent of KBAs within each realm is relatively small when compared to the spatial coverage of VHP and HP areas (see Table 2). Consequently, even a relatively high proportion of overlap with KBAs translates into a modest percentage of the overall priority areas. Second, the criteria used to define KBAs could account for some of the observed mismatch. KBA identification focuses on four main dimensions: (i) presence of threatened biodiversity, (ii) geographically restricted species, (iii) ecological integrity, and (iv) key biological processes (KBA Standards and Appeals Committee of IUCN SSC and IUCN WCPA 2022). These criteria are assessed primarily at the species and population level—considering factors such as conservation status and demographic thresholds—or at the level of ecosystem structure and function. In contrast, our prioritization framework did not incorporate species threat status as a selection variable. Moreover, threatened species do not necessarily represent unique functional or phylogenetic attributes (Mace et al. 2003; González-del-Pliego et al. 2024). Instead, our approach captured broader dimensions of biodiversity, emphasizing environmental variables associated with amphibian diversity, rather than focusing exclusively on species at risk or specific ecosystem types. This conceptual divergence may partially explain the limited spatial overlap between our priority areas and existing KBAs.

4.4. Application of Results Across Spatial Scales

A key limitation of our study lies in its restricted applicability for local and regional (e.g., state, municipality or landscape) scales. Because the analysis was based on global datasets and a relatively coarse spatial resolution (2° hexagons), the resulting priority areas are not intended for direct implementation at finer scales—an issue shared with other global biodiversity prioritization efforts (Myers et al. 2000; Sonne and

Rahbek 2024). Nonetheless, the analytical framework we propose is fully adaptable to smaller spatial extents. All code R required to replicate and modify the analyses is provided in the supplementary materials. Below, we outline a step-by-step protocol to guide adaptation of the method to different spatial resolutions and contexts, summarized in Fig 4.

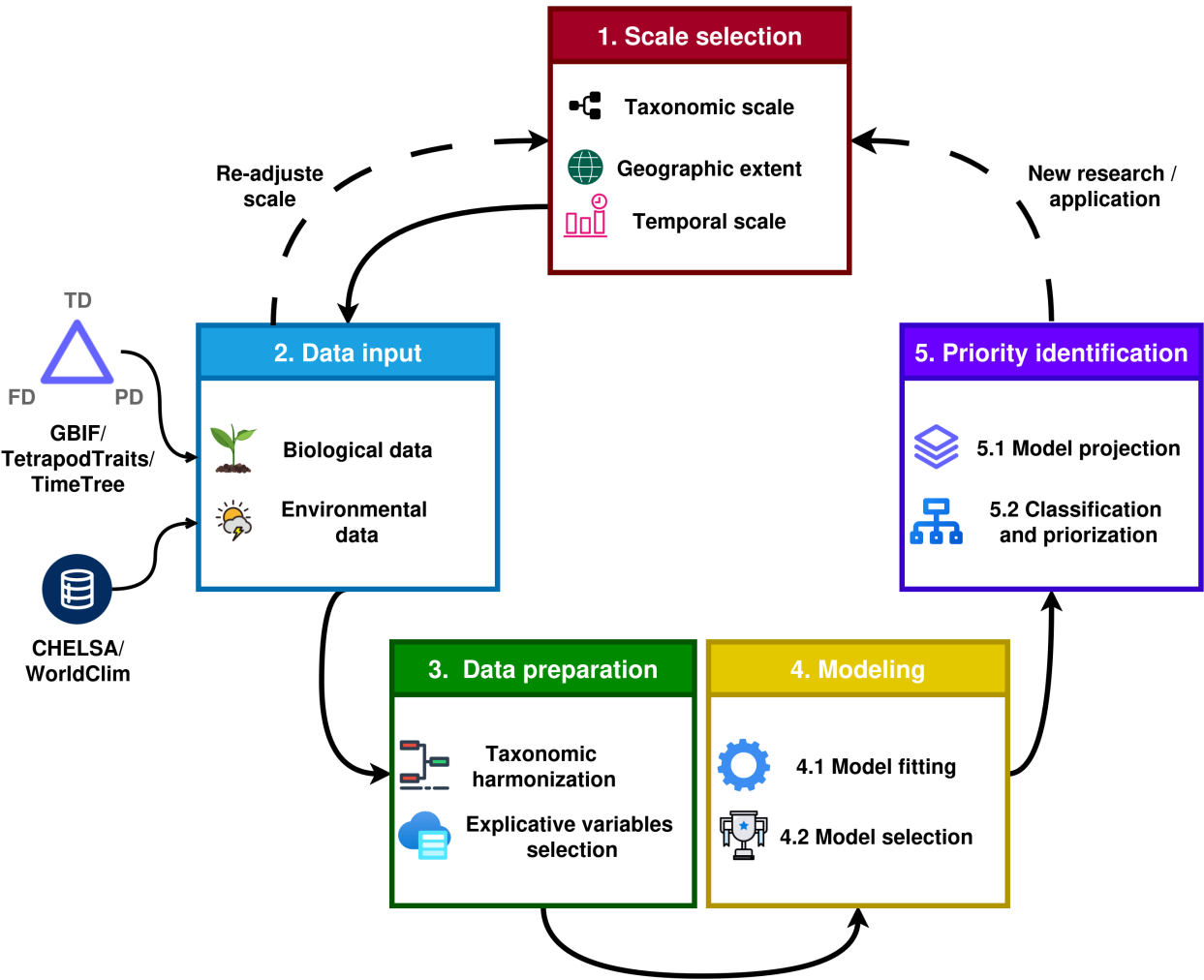


Figure 4. Summary of the application protocol for the identification of priority areas for amphibian conservation at different scales, the details of each step are specified in the text.

1. Scale and regionalization selection: Defining the appropriate scale is one of the most critical preparatory steps. We suggest reflecting on the following questions: What is the taxonomic level of focus in my study—species, genera, or families? What is the

geographic extent—national, regional, or local? Do I have the spatial data and tools necessary to support analyses at that resolution? What is the temporal scope of the study—am I projecting future scenarios or focusing solely on current conditions? In parallel with selecting a geographic extent, consider whether it is important for your results to be distinguished across biogeographic units, such as provinces or biomes. If so, what biogeographic classification system best fits your study region and target group? Clarifying these aspects will allow you to move confidently to the next stage of the analysis.

2. Input data: The analytical framework relies on two main data sources: biological and environmental-climatic datasets. Biological data can be retrieved from global repositories such as GBIF, or from region-specific platforms like SIB (Colombia) and SpeciesLink (Brazil). These are complemented with functional and phylogenetic data, generated using the approach described in this article, which is adaptable to multiple spatial scales. For environmental and climatic data, we recommend databases such as CHELSA or WorldClim, which offer information at various resolutions. To spatially structure the analysis, we strongly advocate for the use of hexagonal grid cells. Environmental variables can be assigned to each cell following the extraction methods detailed in the Methods section. If biological or spatial data are lacking for the selected taxonomic, geographic, or temporal scale, reconsidering the questions from step 1.

3. Data preparation and cleaning: Prior to modeling, both biological and environmental datasets must be thoroughly cleaned and standardized. For biological data, it is essential to perform taxonomic harmonization to prevent the inclusion of duplicate species under different names—an issue that can distort taxonomic,

functional, and phylogenetic assessments. R Packages such as *AmphiNom*, *Taxize*, or the pipeline provided in the supplementary scripts can be employed for this purpose. For environmental variables, collinearity diagnostics are necessary to avoid redundancy and inflated model structures.

4. Modeling: We advise implementing a robust modeling protocol as outlined in the methodology, favoring models with strong predictive performance and limited overfitting. Model selection should rely on criteria such as AIC scores or cross-validation metrics.

5. Projection and prioritization: Once models are validated, outputs can be projected onto the target geographic region, and spatial prioritization can be conducted. Quantile-based classification methods, as described in the Methods, offer a consistent way to identify priority categories. Once the priority areas have been defined, it is possible to return to step 1 and attempt to narrow the spatial, temporal, or taxonomic scope of the analysis in order to address new research questions that remain open.

Following these steps should yield locally relevant conservation priority areas, adjusted to the biodiversity context of each region. These areas are not expected to coincide directly with those identified in this global analysis, as conservation value is inherently relative to the local multidimensional biodiversity structure. Nonetheless, applying the protocol at finer spatial scales should significantly enhance efforts to expand and connect protected areas in alignment with regional conservation planning.

Our study provides a spatially explicit identification of priority areas for conserving amphibian multidimensional diversity globally. The framework we propose moves beyond traditional species-richness approaches by recognizing regionally unique and

diverse areas that may otherwise go unnoticed. While not designed for direct application at local spatial scales, our analytical protocol is adaptable and can support conservation planning at national and subnational levels. By integrating multidimensional metrics and scalable methods, this approach contributes to more integrative and forward-looking conservation strategies—aligned with global biodiversity goals and responsive to the complex challenges of conserving amphibians in a rapidly changing world.

Funding

JMHL was funded with a doctoral scholarship (No. 88887.814811/2023–00) by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). MS acknowledges a research scholarship (MS: 309365/2019–8) by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Competing Interests

The authors have no relevant financial or non-financial interests to declare.

Author Contributions

Jorge Mario Herrera-Lopera: conceptualization (equal), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), writing – original draft (equal), writing – review and editing (equal). Carlos A. Cultid-Medina: conceptualization (equal), formal analysis (equal), investigation (equal), methodology (equal), supervision (equal), writing – original draft (equal), writing – review and editing (equal). Mirco Solé: conceptualization (equal), formal analysis (equal), funding acquisition (equal), investigation (equal), methodology (equal), supervision (equal), writing – original draft (equal), writing – review and editing (equal).

Data Availability

Due to data-sharing restrictions, we are unable to redistribute the original datasets used in this study, including species distributions, functional traits, phylogenetic information, and spatial data of protected and key biodiversity areas. We encourage readers to get these datasets directly from the original sources cited herein. Scripts for data cleaning and curation, as described in the Methods section, are available upon request. All processed datasets and R code essential for reproducing our analyses and results are freely available at Figshare: <https://figshare.com/s/023de1bef294b7b537e6>

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Supplementary Information

We need to protect Amphibians... but where? A global assessment of Priority

Areas based on Multidimensional Diversity

Journal: Diversity and distributions

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Supplementary Information 1: Environmental variables used as predictors to estimate biodiversity metrics in this study. Climate variables were derived from the CHELSA database (Climatologies at High Resolution for the Earth's Land Surface Areas; <https://chelsa-climate.org/>), and elevation data were obtained from WorldClim (<https://www.worldclim.org/>). Geographical coordinates and distances were calculated from the centroids of hexagonal grid cells. Variable names correspond to standard bioclimatic codes and are provided with their respective units and data sources.

Code	Variable	Source	Units
bio1	mean annual air temperature	CHELSA	°C
bio2	mean diurnal air temperature range	CHELSA	°C
bio3	isothermality	CHELSA	%
bio4	temperature seasonality	CHELSA	%
bio5	mean daily maximum air temperature of the warmest month	CHELSA	°C
bio6	mean daily minimum air temperature of the coldest month	CHELSA	°C
bio7	annual range of air temperature	CHELSA	°C
bio8	mean daily mean air temperatures of the wettest quarter	CHELSA	°C
bio9	mean daily mean air temperatures of the driest quarter	CHELSA	°C
bio10	mean daily mean air temperatures of the warmest quarter	CHELSA	°C
bio11	mean daily mean air temperatures of the coldest quarter	CHELSA	°C
bio12	annual precipitation amount	CHELSA	mm
bio13	precipitation amount of the wettest month	CHELSA	mm
bio14	precipitation amount of the driest month	CHELSA	mm
bio15	precipitation seasonality	CHELSA	%
bio16	mean monthly precipitation amount of the wettest quarter	CHELSA	mm
bio17	mean monthly precipitation amount of the driest quarter	CHELSA	mm
bio18	mean monthly precipitation amount of the warmest quarter	CHELSA	mm
bio19	mean monthly precipitation amount of the coldest quarter	CHELSA	mm
npp	Net primary productivity	CHELSA	g C m ⁻² yr ⁻¹
x	Longitude	Hexagon centroid	Decimal degrees (WGS84)
y	Latitude	Hexagon centroid	Decimal degrees (WGS84)
elevation	Elevation in meters	WorldClim	meters
Distance	Geodesic distance, only for beta diversity models.	Coordinates distance	meters

Supplementary Information 2: Summary of the best generalized linear models (GLMs) selected for each alpha diversity metric across biogeographic realms. For each model, the distribution family and link function used are indicated. Predictor variables are listed with their estimated slope and associated p-values. ΔAICc indicates the difference in corrected Akaike Information Criterion between the selected model and its corresponding null model (intercept-only). Null models were fitted using the same distribution family as their respective best model. Variable names follow the codes defined in Supplementary Information 1.

Species richness ($^{\circ}\text{TD}$)			
<i>Nearctic – Distribution family: Negative binomial</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	4.07	0.00	413.96
x	0.01	0.01	
y	-0.05	0.00	
bio10	0.05	0.00	
bio13	0.00	0.00	
bio17	0.00	0.00	
bio8	-0.01	0.01	
<i>Neotropic – Distribution family: Negative binomial</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	2.10	0.00	156.32
y	0.00	0.10	
bio15	-0.01	0.00	
bio16	0.00	0.00	
bio18	0.00	0.00	
bio19	0.00	0.00	
bio2	0.12	0.00	
bio4	0.00	0.00	
<i>Afrotropic – Distribution family: Negative binomial</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	3.07	0.00	80.93
y	-0.01	0.00	
bio13	0.00	0.00	
bio15	-0.01	0.00	
<i>Palaearctic – Distribution family: Negative binomial</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	1.31	0.08	46.87
y	-0.02	0.02	
bio1	-0.04	0.00	
bio15	-0.01	0.01	
bio3	3.56	0.00	

bio8	0.03	0.00	
npp	0.00	0.00	
<i>Indo-Malayan – Distribution family: Negative binomial</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	0.67	0.18	23.6
x	0.03	0.00	
y	-0.01	0.09	
bio17	0.00	0.01	
<i>Australasia – Distribution family: Negative binomial</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	-1.59	0.00	122.04
x	0.03	0.00	
bio15	0.01	0.00	
bio16	0.00	0.00	
bio8	-0.03	0.00	
elev	0.00	0.00	
Functional group richness (⁰FD)			
<i>Nearctic – Distribution family: Gamma (link = “log”)</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	3.65	0.11	330.52
x	0.08	0.00	
bio10	0.29	0.00	
bio13	0.01	0.00	
bio17	0.01	0.00	
bio8	0.09	0.01	
bio9	0.08	0.00	
elev	0.00	0.01	
<i>Neotropic – Distribution family: Gamma (link = “log”)</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	1.57	0.00	175.41
y	0.01	0.00	
bio15	-0.01	0.00	
bio16	0.00	0.00	
bio18	0.00	0.00	
bio19	0.00	0.00	
bio2	0.06	0.00	
bio4	0.00	0.00	
<i>Afrotropic – Distribution family: Gamma (link = “log”)</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	2.05	0.00	90.62
y	-0.01	0.00	
bio13	0.00	0.00	
bio15	-0.01	0.00	
bio18	0.00	0.03	
<i>Palaearctic – Distribution family: Gamma (link = “log”)</i>			
Predictor	Slope	p-value	ΔAICc with Null model
Intercept	0.72	0.18	63.29
y	-0.02	0.00	
bio1	-0.02	0.00	

bio15	-0.01	0.00
bio3	3.09	0.00
bio8	0.03	0.00
npp	0.00	0.00

Indo-Malayan – Distribution family: Gamma (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	-7.34	0.01	27.27
x	0.18	0.00	
bio17	0.00	0.09	

Australasia – Distribution family: Gamma (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	-0.75	0.03	109.33
x	0.02	0.00	
bio15	0.00	0.00	
bio16	0.00	0.00	
bio8	-0.02	0.00	
elev	0.00	0.02	

Lineage richness (°PD)

Nearctic – Distribution family: Inverse Gaussian (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	2.35	0.03	323.38
x	0.04	0.00	
bio10	0.17	0.00	
bio13	0.01	0.00	
bio17	0.01	0.00	
bio9	0.04	0.00	
elev	0.00	0.00	

Neotropic – Distribution family: Gamma (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	0.71	0.00	148.6
y	0.01	0.01	
bio15	-0.01	0.00	
bio16	0.00	0.00	
bio18	0.00	0.00	
bio19	0.00	0.00	
bio2	0.08	0.00	
bio4	0.00	0.00	

Afrotropic – Distribution family: Gamma (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	1.55	0.00	60.33
y	-0.01	0.02	
bio13	0.00	0.00	
bio15	-0.01	0.00	

Palaearctic – Distribution family: Gamma (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	0.53	0.01	48.73
bio1	-0.02	0.00	
bio15	0.00	0.01	
bio2	0.10	0.00	

bio4	0.00	0.00
bio8	0.02	0.00
npp	0.00	0.00

Indo-Malay – Distribution family: Gamma (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	0.03	0.94	20.08
x	0.02	0.00	
y	-0.01	0.10	
bio17	0.00	0.01	

Australasia – Distribution family: Inverse Gaussian (link = “log”)

Predictor	Slope	p-value	ΔAICc with Null model
Intercept	-0.47	0.04	139.45
x	0.01	0.00	
bio15	0.00	0.05	
bio16	0.00	0.00	
bio8	-0.01	0.00	
elev	0.00	0.01	

Supplementary Information 3: Predictive performance of random forest best models for each beta diversity dimension (taxonomic, functional, and phylogenetic) across the six terrestrial biogeographic realms. MSE (Mean Squared Error) indicates the average squared difference between observed and predicted values. R^2 (coefficient of determination) was calculated by comparing the predicted values against the observed values using the classical approach, and represents the proportion of variance in the observed beta diversity values explained by the model. The explained variance (%) corresponds to the percentage of variance explained by the model, as estimated from the out-of-bag (OOB) error, which provides an internal validation similar to cross-validation.

Beta diversity dimension	Realm	MSE	R^2	Explained variance (%)
Taxonomic – $T\beta_{total}$	Nearctic	0.00	0.81	81.92
	Neotropic	0.00	0.86	86.75
	Afrotropic	0.00	0.82	83.37
	Palearctic	0.01	0.74	76.90
	Indo-Malay	0.00	0.89	87.81
	Australasia	0.00	0.83	82.42
Functional – $F\beta_{total}$	Nearctic	0.01	0.73	72.78
	Neotropic	0.01	0.61	61.27
	Afrotropic	0.01	0.59	56.93
	Palearctic	0.01	0.62	62.21
	Indo-Malay	0.01	0.73	64.45
	Australasia	0.01	0.67	64.15
Phylogenetic – $P\beta_{total}$	Nearctic	0.01	0.70	69.99
	Neotropic	0.00	0.71	70.72
	Afrotropic	0.01	0.68	70.40
	Palearctic	0.01	0.60	63.29
	Indo-Malay	0.01	0.74	70.01
	Australasia	0.01	0.82	82.03

Capítulo 3

Holding the Line on Amphibian Conservation: Mapping Stable Priority Areas in a Changing World

Manuscrito preparado para submeter em Perspectives in Ecology and Conservation (PECON) -

ISSN: 2530-0644



Siphonops annulatus – Yang Wong

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“We’re not doing a very good job as stewards of our environment. We abuse our surroundings and pay the consequences with decreased quality of life and physical and psychological health issues. In addition to hurting ourselves, we destroy and pollute habitat for wildlife and threaten their future through human- induced climate change. Seven generations from now, our descendants may read about staghorn coral, leatherback sea turtles, emperor penguins, and polar bears, but never see them alive”.

“Não estamos fazendo um bom trabalho como guardiões do nosso meio ambiente. Abusamos do nosso entorno e pagamos as consequências com diminuição da qualidade de vida e problemas de saúde física e psicológica. Além de prejudicarmos a nós mesmos, destruímos e poluímos o habitat da vida selvagem e ameaçamos seu futuro por meio das mudanças climáticas induzidas pelo homem. Daqui a sete gerações, nossos descendentes poderão ler sobre corais-chifre-de-veado, tartarugas-de-couro, pinguins-imperadores e ursos-polares, mas nunca os verão vivos”.

Marty Crump

Holding the Line on Amphibian Conservation: Mapping Stable Priority Areas in a Changing World

Revista: Perspectives in Ecology and Conservation

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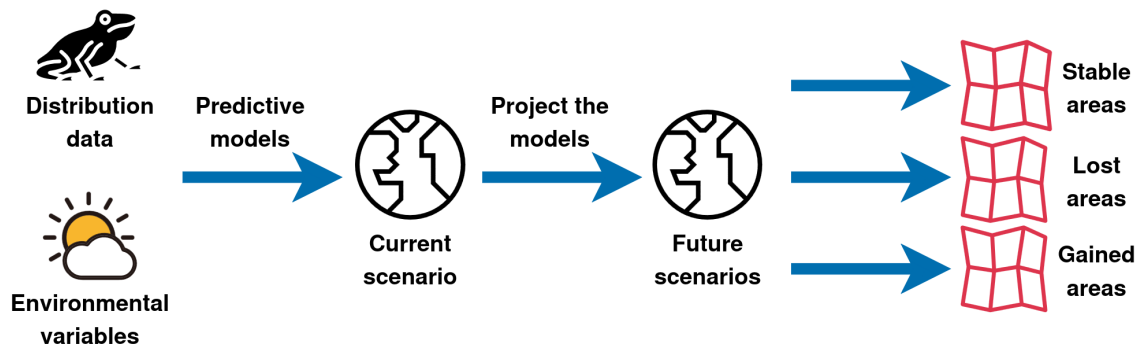
Acknowledgments

This study was built upon the collective work of countless researchers, curators, and naturalists who gather and share biodiversity data. We are deeply grateful to this global community for making conservation science a collaborative endeavor.

Funding

JMHL was funded with a doctoral scholarship (No. 88887.814811/2023–00) by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). MS acknowledges a research scholarship (MS: 309365/2019–8) by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Graphical abstract



Abstract

Climate change threatens global amphibian diversity, the most endangered vertebrate group, mainly due to habitat loss. We assessed how climate change affects amphibian conservation priority areas across six biogeographic realms by integrating taxonomic, functional, and phylogenetic diversity dimensions. Using present-day environmental predictors and three future climate scenarios (SSP1-2.6, SSP3-7.0, SSP5-8.5), we identified Very High Priority (VHP) areas, (i.e., regions with the highest multidimensional diversity). We quantified spatial shifts between current and future priorities, distinguishing stable, gained, and lost VHP areas, and evaluated their overlap with current protected areas. Contrary to our expectations, stable VHP areas showed no significant disparity between tropical and temperate realms. Most current priority regions (70.6–93.4% across realms) remained stable across all scenarios, though their total extent declined. Protection coverage of stable areas decreased relative to present conditions, most sharply under pessimistic scenarios. While total protected area did not differ significantly between tropical and temperate realms, stable areas consistently exhibited reduced protection across future scenarios. We propose

that these stable VHP areas may serve as strategic focal regions for strengthening protected area networks and enhancing landscape connectivity between them, thereby improving long-term amphibian resilience to climate change.

Highlights:

Most amphibian priority areas persist across climate scenarios.

Stable areas loss protection, especially in pessimistic futures.

Tropical and temperate realms show similar stability patterns.

Multidimensional approach captures overlooked diversity areas.

Introduction

For a species to persist within a given region, it must encounter favorable biotic and abiotic conditions, be able to disperse to that region, and successfully adapt to it (Soberon and Peterson, 2005). Climate change alters temperature and precipitation regimes across spatial and temporal scales, directly modifying abiotic conditions and indirectly affecting biotic ones through the restructuring of local communities (Hannah et al., 2007; Rosenfield et al., 2025; Wake and Vredenburg, 2008). Understanding how these modifications unfold over space and time is essential for designing effective strategies to conserve biodiversity under ongoing climatic change (Hannah, 2008; Mi et al., 2023).

Protected areas, as the primary tool for *in situ* biodiversity conservation, remain the most effective means to safeguard species, maintain ecosystem functions, and preserve evolutionary trajectories (Hannah et al., 2007; Quan et al., 2018). Although their importance as refuges for species under future climate scenarios has been demonstrated (Mi et al., 2023), biodiversity conservation must go beyond species richness or the preservation of portions of species' ranges (Araújo and Rahbek, 2006; Rosenfield et al., 2025). It should also ensure the protection of ecological functions and evolutionary lineages within ecosystems (Gumbs et al., 2021; Margules and Pressey, 2000).

The impact of climate change on protected areas is unlikely to be uniform across the globe. Although tropical species typically exhibit narrower environmental tolerances than those from temperate regions (Wake and Vredenburg, 2008), tropical ecosystems have historically shown greater biodiversity stability. This stability is not due to the absence of environmental variability, but rather to dynamic processes of extinction and colonization among ecologically similar species with overlapping environmental

niches, which enable communities to persist through continuous species turnover (Hooghiemstra et al., 2002). Conversely, temperate regions host assemblages dominated by species with broader environmental tolerances, adapted to pronounced seasonality and exhibiting lower niche overlap, which constrains compositional turnover. In such contexts, climate change may have stronger impacts, rendering currently warm regions increasingly inhospitable through rising temperatures and hydric stress, while making presently cold areas more suitable under milder climatic conditions (Araújo et al., 2006).

Amphibians represent the most threatened group of vertebrates, with over 40% of species currently facing extinction risk, mainly driven by habitat loss (Luedtke et al., 2023). While some studies propose that protected areas may function as climatic refugia for amphibians under ideal dispersal scenarios (Araújo et al., 2006; Mi et al., 2023), others highlight that climate change could disrupt not only species distributions but also other dimensions of amphibian diversity (Alves-Ferreira et al., 2025). In line with the Kunming–Montreal Global Biodiversity Framework, which prioritizes the conservation of biodiversity in its broadest sense, not solely the protection of species (Kunming-Montreal Global Biodiversity Framework, 2022), our conservation strategies should aim to identify regions concentrating the highest multidimensional diversity (species, functions, and lineages), evaluate their stability under future climatic conditions, and reinforce protection networks within the most persistent areas.

We aimed to identify and map amphibian conservation priority areas that remain stable under optimistic, moderate, and pessimistic climate scenarios across biogeographic realms. We further evaluated the proportion of these stable priority areas falling within protected areas. We hypothesized that tropical realms (Afrotropic, Neotropic and

Indomalayan) would retain a higher proportion of stable areas compared to temperate realms (Australasia, Nearctic, and Palearctic), where climate change is likely to cause stronger spatial shifts in conservation priorities. We also expected that, despite their higher multidimensional diversity, tropical realms would exhibit lower protection coverage of climatically stable priority areas.

Methods

Biogeographic regionalization, extent, and spatial resolution

We followed the biogeographic framework of Dinerstein et al. (2017) to define the realms analyzed in this study. Oceania was excluded due to its negligible representation (0.03% of records), and Antarctica because it lacks amphibians. Consequently, six realms were retained: Afrotropic, Australasia, Indo-Malayan, Nearctic, Neotropic, and Palearctic. To avoid bias from areas unsuitable for amphibians, we clipped these realms with a mask derived from the IUCN (2024) amphibian distribution polygons. Each realm was then divided into hexagonal units (2° width; ~222.64 km at the equator), generated with functions from the R packages *sf*, *terra*, and *tidyterra* (Hernangómez, 2023; Hijmans, 2024; Pebesma, 2018; R Core Team, 2025).

Data acquisition

We obtained amphibian records from GBIF, retaining only georeferenced museum-supported entries to reduce misidentifications (DOI: GBIF.Org, 2024). After curation and taxonomic updates, the dataset included 5,350 species from 523 genera and 72 families. Functional traits were compiled from Moura et al. (2024) and Oliveira et al. (2017), including activity pattern (diurnal, nocturnal, or both), habitat use (terrestrial, arboreal, aquatic, fossorial, or combinations), body size (snout–vent length), body

mass, and reproductive strategy (direct development, larval stage, or viviparity). These traits were chosen for their ecological relevance (Cortes Gómez et al., 2016). The phylogenetic tree was obtained from TimeTree 5 (Kumar et al., 2022). All procedures for data cleaning, taxonomic updates, and gap-filling for functional and phylogenetic information are detailed in Supplementary Material 1.

Global predictors and climate scenarios

We used 20 environmental variables from CHELSA v2.1 (Karger et al., 2021b), including bioclimatic indices (Bio1–Bio19) and net primary productivity, complemented with elevation (WorldClim; Fick and Hijmans, 2017) and centroid latitude/longitude of each hexagon. Details of variable definitions and averaging protocols are given in Supplementary Material 2.

Future conditions were derived from CHELSA projections for 2100 (Karger et al., 2021a) under three Shared Socioeconomic Pathways (SSPs): SSP1–2.6 (optimistic), SSP3–7.0 (moderate), and SSP5–8.5 (pessimistic). For each, we averaged outputs from three Global Climate Models (GCMs: GFDL-ESM4, UKESM1-0-LL, and MPI-ESM1-2-HR) to generate a unified predictor set. Scenario descriptions, GCM information, and processing steps are detailed in Supplementary Material 3.

Data analysis

We calculated zero-order diversity (0D) as a measure of alpha diversity for taxonomic (0TD), functional (0FD), and phylogenetic (0PD) dimensions of each hexagon with sufficient data using the R package *iNEXT.3D* (Chao, 2024). Beta diversity, including taxonomic ($T\beta$), functional ($F\beta$), and phylogenetic ($P\beta$), was estimated for all hexagon pairs within each realm using the R package *BAT* (Cardoso et al., 2014). To ensure reliability, diversity measures were computed only for hexagons containing at least

three species and more than three records. Further details on the diversity dimensions and calculation procedures are provided in Supplementary Material 4.

We predicted amphibian diversity across the full extent using hexagons with sampling coverage above 0.5 for the previously calculated alpha and beta diversity measures. Random Forest models were fitted for each diversity dimension using the R package *randomForest* (Breiman et al., 2002), with CHELSA variables from the "*Global predictors and climate scenarios*" section as predictors. The models were adjusted and projected independently for each biogeographical realm. Detailed protocols for model fitting and performance metrics are provided in Supplementary Material 5 and metrics for the models used are shown in Supplementary Material 6.

RandomForest models were projected for the current climate scenario used to fit the models, as well as for each future climate scenario. Because beta diversity is meaningful only when comparing pairs of hexagons, and comparisons between very distant hexagons are less relevant due to expected spatial variation, we defined beta diversity for each hexagon as the average dissimilarity with its adjacent neighbors (those sharing a border). For isolated hexagons without direct neighbors, such as small islands, no beta diversity value was assigned to avoid overestimation.

Priority areas were defined as hexagons exhibiting the highest multidimensional alpha and beta diversity (taxonomic, functional, and phylogenetic) within each realm. To combine these measures, we first standardized values between 0 and 1. For each dimension, we calculated the difference (delta) between each hexagon's diversity and the maximum value observed within its realm. The summed deltas were used to derive an overall diversity score, where hexagons with the lowest delta values were closest to the realm's maximum diversity. Hexagons were then classified into four priority levels

based on quantiles: “Very High” (VHP) for hexagons with the smallest differences, followed by “High” (HP), “Medium” (MP), and “Low” (LP) for hexagons with the greatest differences. For isolated hexagons lacking beta diversity values (about 68 hexagons, 1.4% of the total), priority classification was based solely on alpha diversity.

We assessed changes in the highest-priority areas (VHP) for each realm between the current and future climate scenarios using a spatial match analysis (Nori et al., 2020). Areas that were priorities in the present but not in future scenarios were considered losses, areas that were not priorities in the present but became priorities in the future were considered gains, and areas that remained priorities across scenarios were considered stable. The same spatial match approach was used to evaluate overlap between VHP and protected areas (PAs), obtained from The World Database on Protected Areas (UNEP-WCMC and IUCN, 2023). Analyses were performed separately for each realm with a global equal-area projection (Eckert IV, ESRI:54012) to ensure accurate spatial representation. All computations were conducted in R packages *terra* and *tidyterra* (Hernangómez, 2023; Hijmans, 2024).

Results

Present-day priority areas for amphibian conservation were clustered within specific subregions of each realm (Fig. 1 - Present). In the Afrotropic, they concentrated around the equatorial belt and eastern Madagascar. In Australasia, they occurred in eastern Australia, New Zealand, and Papua New Guinea. Indo-Malayan priority areas were found in the forests of Southeast Asia, particularly the Indochinese Peninsula. In the Nearctic, they extended from central Mexico to the southern United States, forming a “V” pattern toward the coasts. Neotropical priority areas were concentrated in the

Northern Andes and the Brazilian Atlantic Forest. In the Palearctic, they were located in the Mediterranean Basin, parts of China's transitional zone, and western Europe.

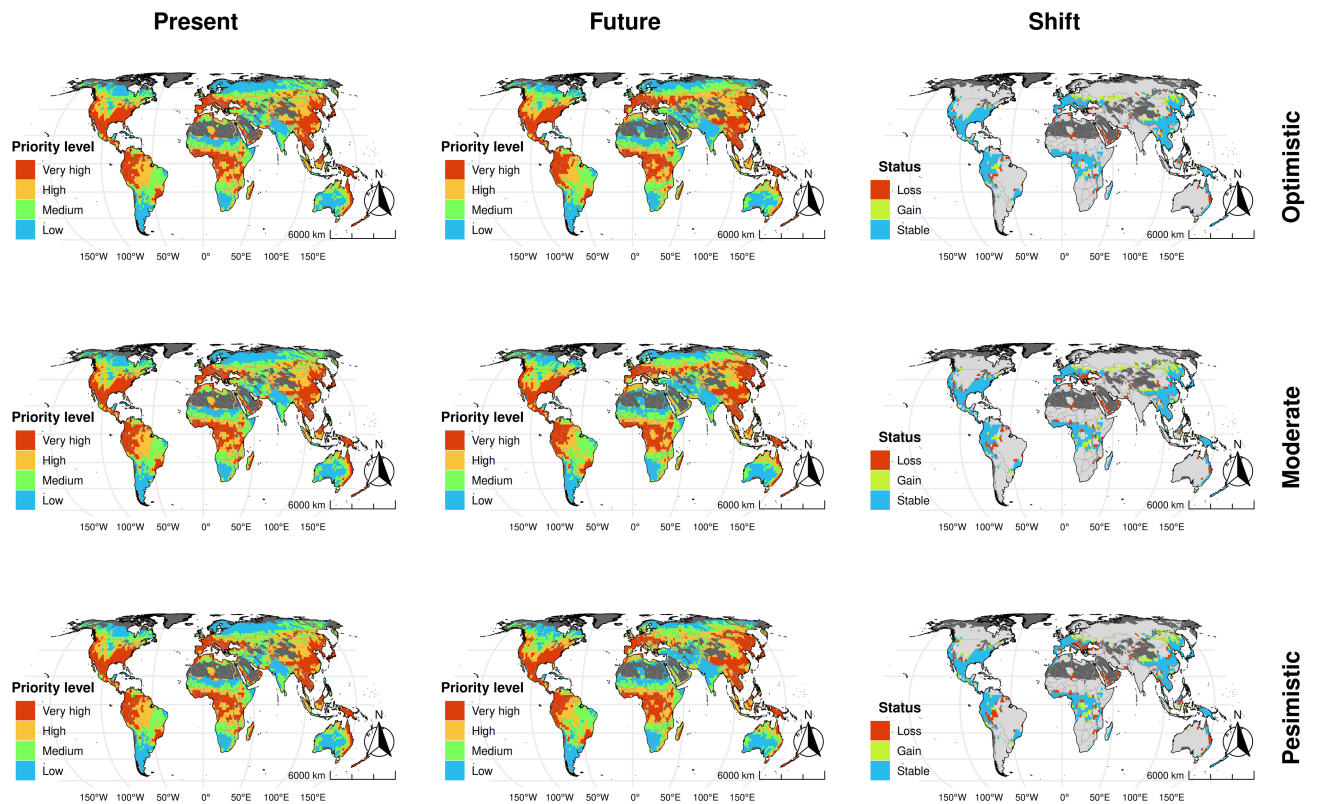


Figure 1. Amphibian conservation priority areas (areas of highest multidimensional diversity) under optimistic, moderate and pessimistic climate scenarios and the shift relative to current scenario. Gain areas (third column) represent regions that were not classified as Very High Priority (VHP) under the present scenario but become VHP in the future. Loss areas are those that were VHP in the present but lose this status under future scenarios. Stable areas remained VHP in both the present and future scenarios.

Across all three climate scenarios, the spatial distribution of Very High Priority (VHP) areas changed relative to the present (Table 1). Despite differences in the magnitude of change among realms, a consistent pattern emerged: stable areas dominated, indicating that most current priority regions are likely to remain important under future conditions (Fig. 1). However, we detected no significant differences in the loss of present-day VHP areas between tropical and temperate realms across future

scenarios. Furthermore, although the total extent of stable areas was significantly smaller than that of current priority areas, no significant differences were observed among the three climate scenarios in the proportion of area lost (Fig. 2A).

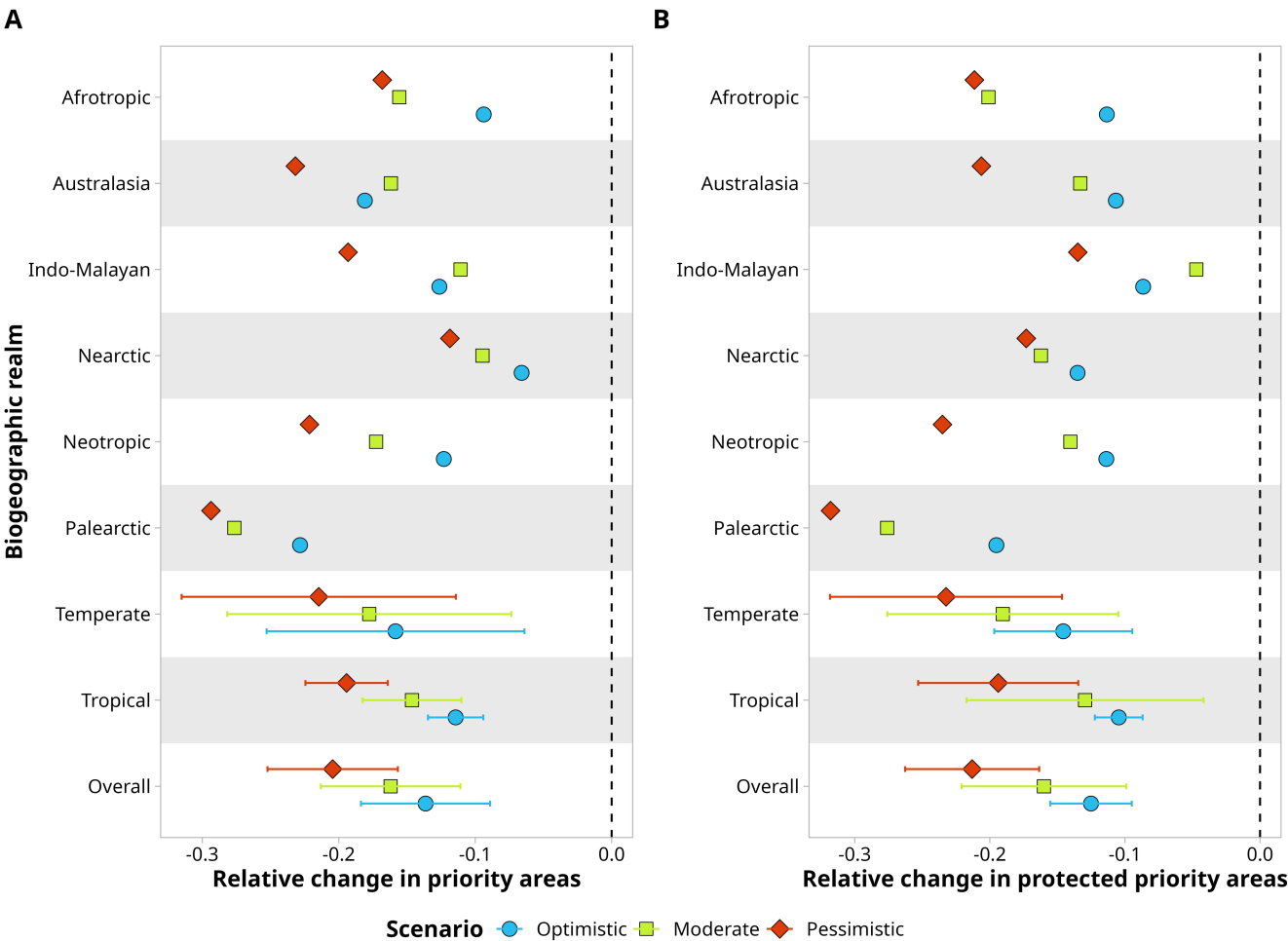


Figure 2. Changes in stable areas relative to Very High Priority (VHP) areas across biogeographic realms under optimistic, moderate and pessimistic climate scenarios. (A) Change relative to area extent. (B) Change relative to protection coverage. Temperate includes the Australasia, Nearctic, and Palearctic realms, while Tropical includes the Afrotropic, Indo-Malayan, and Neotropic realms. Both these categories, as well as Overall, which represents all biogeographic realms, show mean values with 95% confidence intervals.

Losses of priority areas ranged from 0.05% in Australasia (moderate scenario) to 32.97% in the Palearctic (pessimistic). Gains, defined as areas becoming priorities under future scenarios, ranged from 1.96% in Australasia (moderate) to 31.67% in the

Paleartic (moderate). Stable areas, which remained priorities across scenarios, ranged from 70.63% in the Palearctic (pessimistic) to 93.4% in the Nearctic (optimistic). Spatially, most priority areas remained stable across scenarios. Nevertheless, a consistent trend across realms was observed: equatorial regions and warm regions such as the Mediterranean, northeastern Australia, or the southern United States and Mexico, tended to lose high-priority status, while some higher-latitude areas gained priority (Fig. 1).

Table 1. Loss, Gain, and Stable Very High Priority (VHP) areas across biogeographic realms under optimistic, moderate and pessimistic climate scenarios. Area values are given in million hectares (Mha).

	Loss – area (%)			Gain – area (%)			Stable – area (%)		
	Optimistic	Moderate	Pessimistic	Optimistic	Moderate	Pessimistic	Optimistic	Moderate	Pessimistic
Afrotropic	40.31 (7.2)	67.17 (11.99)	69.26 (12.37)	51.97 (9.28)	82.52 (14.74)	82.44 (14.72)	507.55 (90.63)	472.87 (84.43)	465.88 (83.19)
Australasia	0.97 (0.54)	0.08 (0.05)	5.05 (2.82)	6.76 (3.78)	3.51 (1.96)	16.89 (9.43)	146.72 (81.91)	150.14 (83.82)	137.6 (76.82)
Indo-Malayan	40.21 (17.48)	39.32 (17.1)	50.25 (21.85)	38.06 (16.55)	35.95 (15.63)	45 (19.57)	200.94 (87.37)	204.51 (88.92)	185.55 (80.68)
Nearctic	59 (11.5)	73.93 (14.41)	86.09 (16.78)	66.53 (12.97)	63.1 (12.3)	66.34 (12.93)	479.1 (93.4)	464.39 (90.53)	452.13 (88.14)
Neotropic	50.19 (9.23)	78.75 (14.49)	114.54 (21.07)	51.32 (9.44)	67.21 (12.36)	78.49 (14.44)	476.74 (87.7)	449.75 (82.73)	423.2 (77.85)
Palearctic	252.98 (25.23)	302.12 (30.13)	330.62 (32.97)	261.81 (26.11)	317.56 (31.67)	296.97 (29.62)	773.69 (77.16)	725.38 (72.34)	708.22 (70.63)

Across all climate scenarios, stable areas exhibited lower protection coverage compared to current priority areas. However, no significant differences were detected between tropical and temperate realms in the magnitude of these reductions across climate scenarios. Overall, protection declined less under the optimistic scenario than under the pessimistic one, with the moderate scenario showing intermediate values (Fig. 2B).

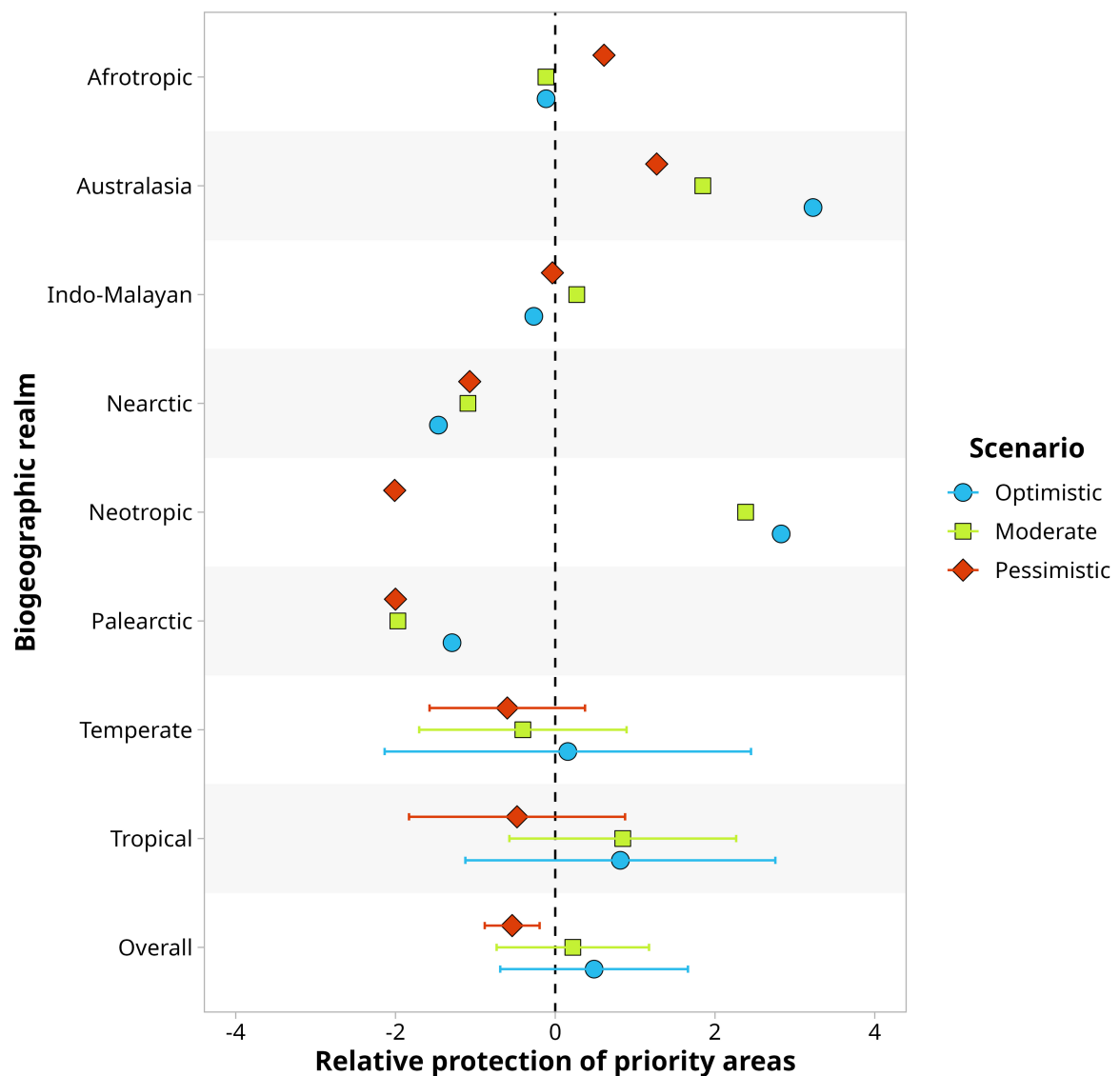


Figure 3. Protection of Very High Priority (VHP) areas across biogeographic realms under optimistic, moderate and pessimistic climate scenarios. Temperate includes the Australasia, Nearctic, and Palearctic realms, while Tropical includes the Afrotropic, Indo-Malayan, and Neotropic realms. Both categories, as well as Overall, which represents all biogeographic realms, show mean values with 95% confidence intervals.

When considering all priority areas predicted under each scenario, protection levels varied across realms. However, no significant differences were detected between temperate and tropical realms, either in comparison with the present or between each other (Table 2). Overall, total protection decreased under the pessimistic scenario,

while the moderate and optimistic scenarios showed no significant change relative to current scenario (Fig. 3).

Table 2. Loss in protection and area represented by stable areas relative to the Very High Priority (VHP) areas in the present scenario. Area values are given in million hectares (Mha). Pas: Protected areas, PPP: Protected priority areas in present scenario.

	PAs area	PPP	Stable areas			Priority area protected – area (%)			Protected area loss – area (%)		
			Optimistic	Moderate	Pessimistic	Optimistic	Moderate	Pessimistic	Optimistic	Moderate	Pessimistic
Afrotropic	465.76	122.97	507.55	472.87	465.88	109.02 (21.48)	98.25 (20.78)	96.97 (20.81)	13.95 (11.34)	24.72 (20.1)	26 (21.14)
Australasia	200.95	37.41	146.72	150.14	137.60	33.41 (22.77)	32.43 (21.6)	29.69 (21.58)	3.99 (10.67)	4.98 (13.31)	7.72 (20.63)
Indomalayan	73.32	34.13	200.94	204.51	185.55	31.18 (15.52)	32.52 (15.9)	29.52 (15.91)	2.95 (8.65)	1.61 (4.72)	4.6 (13.49)
Nearctic	215.32	61.54	479.10	464.39	452.13	53.23 (11.11)	51.56 (11.1)	50.89 (11.26)	8.31 (13.51)	9.98 (16.22)	10.65 (17.31)
Neotropic	595.00	235.32	476.74	449.75	423.20	208.55 (43.75)	202.29 (44.98)	180.01 (42.53)	26.78 (11.38)	33.03 (14.04)	55.32 (23.51)
Palaearctic	529.68	195.47	773.69	725.38	708.22	157.33 (20.33)	141.52 (19.51)	133.33 (18.83)	38.14 (19.51)	53.95 (27.6)	62.14 (31.79)

Discussion

Most current amphibian priority areas remained stable across biogeographic realms and under all projected climate scenarios. Contrary to our expectations, stability was not greater in tropical realms but instead remained consistently high across both tropical and temperate regions. Likewise, protection levels of stable areas differed among realms but did not exhibit a clear tropical–temperate gradient. Although the greatest reduction in protected stable areas from present to future conditions occurred within a temperate realm, no significant differences were detected between tropical and temperate realms across climate scenarios.

The Very High Priority (VHP) areas for amphibian conservation identified in this study broadly overlap with the biodiversity hotspots proposed by Mittermeier et al., (2004, 2011) and Hoffman et al. (2016), as many global hotspots coincide spatially with our VHP areas. However, substantial discrepancies exist across realms, since some

regions within recognized hotspots are not classified as VHP areas, while several VHP areas fall outside traditional hotspot boundaries. These mismatches likely reflect the influence of additional dimensions of diversity beyond species richness, which can reveal biologically significant regions that richness-based approaches alone might overlook. Similar patterns have been reported in studies incorporating functional or phylogenetic diversity across different taxa (e.g., Fritz and Rahbek, 2012; Robroek et al., 2017; Xu et al., 2024). Together, these results highlight that different diversity metrics are not interchangeable but complementary, each revealing unique ecological and evolutionary processes. Therefore, adopting a multidimensional approach is not only desirable but necessary to ensure that conservation planning effectively captures the full spectrum of amphibian biodiversity.

Across all future climate scenarios, the distribution of VHP areas for amphibian conservation changes relative to the present. The general pattern indicates that most currently prioritized areas remain so under future conditions, forming stable areas. As expected, the optimistic scenario shows the smallest changes, followed by the moderate and the pessimistic scenarios. Areas that lose their priority status (loss areas) likely become unsuitable (based on the environmental predictors used) to sustain the current levels of amphibian diversity. Conversely, areas that gain priority (gain areas) are those projected to become more suitable for amphibians in the future. The loss of suitable areas has been widely documented for amphibians and is often linked to declining habitat suitability for species near their thermal or hydric limits, particularly in tropical and warm regions (Alves-Ferreira et al., 2025; Deutsch et al., 2008; Lawlor et al., 2024). The interpretation of gain areas, however, requires caution. As Soberon and Peterson (2005) emphasized, a species' occurrence depends on four

fundamental components: favorable abiotic and biotic conditions, dispersal ability, and adaptive capacity. While gain areas may meet the first two conditions, their future occupancy will depend on the ability of species to reach and persist in them. Given the generally low dispersal capacity of amphibians, often limited to a few hundred meters and rarely exceeding tens of kilometers (Blaustein et al., 1994; Smith and Green, 2005), many of these potential gains may represent theoretical rather than real opportunities for range expansion. Therefore, conservation attention should primarily focus on stable areas, which are important both now and under future climatic conditions. These areas do not imply security but rather highlight where local-scale studies are urgently needed to identify and map amphibian diversity and threats, and to strengthen conservation networks within them (Araújo et al., 2006; Mittermeier et al., 2004).

Although most present-day priority areas are projected to remain stable across future climate scenarios, their total extent is considerably reduced. These stable regions should not be viewed as static environmental refugia, but rather as dynamic systems where species persistence is possible through processes such as altitudinal or latitudinal shifts, turnover, and colonization, resembling the ecological dynamics that maintain tropical forest diversity (Hooghiemstra et al., 2002). While such processes could occur under an idealized scenario of unlimited dispersal (Araújo et al., 2006), they are far less feasible in real-world landscapes where amphibians have limited movement capacity, are often philopatric, and face strong connectivity barriers imposed by urbanization, intensive agriculture, and hydrologically stressed environments (Blaustein et al., 1994). Consequently, the loss of any currently prioritized area under future conditions could have severe implications for amphibian

diversity persistence. All climate scenarios exhibited this general trend of area reduction. Stable regions, however, can be strategically used to guide local-scale conservation planning, similar to the function of biodiversity hotspots (Mittermeier et al., 2011), serving as focal zones to assess existing protection levels and to design connectivity strategies through new protected areas or amphibian-friendly matrices (Pinzón et al., 2025; Volkmer et al., 2025). Applying least-cost path modeling could further identify where reducing landscape resistance would most effectively sustain the ecological integrity of these stable regions under climate change.

Across all future climate scenarios, current VHP areas are projected to experience a decline in protection coverage. Although this reduction varies among realms, future VHP areas generally maintain similar protection levels to those of the present, except under the pessimistic scenario, which shows a clear decrease. These results contrast with findings by Mi et al. (2023), who predicted an increase in amphibian protection under climate change when analyses were based on species range models. This discrepancy likely arises because our approach integrates multiple dimensions of diversity, revealing that while species richness might remain stable or even increase within protected areas, other facets, such as functional or phylogenetic diversity, may not receive equivalent protection. Beyond the boundaries of current reserves, it becomes essential to evaluate the stability and connectivity of priority areas under future climates. Establishing new protected areas or developing buffer zones and amphibian-friendly landscape matrices (Pinzón et al., 2025) that enhance dispersal and colonization between reserves could play a key role in mitigating climate change impacts on amphibian diversity.

Our study provides a global-scale assessment of the multidimensional diversity response of amphibians, identifying areas of stability and change relative to current conservation priorities. Although these results offer valuable insights, they should not be interpreted as directly applicable at the management level, as stable areas often span broad regions that may include several countries. Instead, these areas should serve as a strategic guide, much like biodiversity hotspots (Mittermeier et al., 2011), to help prioritize conservation and connectivity actions in regions with the potential to remain highly diverse under future climate conditions. Further work at finer spatial scales is essential to determine which of these stable areas are genuinely viable for conservation, after accounting for urban expansion, intensive land use, and other anthropogenic pressures. Within these zones, research and management efforts should also focus on identifying land-use matrices and agricultural landscapes that could facilitate amphibian dispersal and genetic exchange among populations. While climate change will inevitably alter environmental conditions, proactively identifying and managing stable and connected regions could substantially improve the long-term conservation prospects for global amphibian diversity and reduce the costs associated with the loss of ecosystem functions and delayed conservation actions (Araújo and Rahbek, 2006; Hannah et al., 2007).

Competing Interests

The authors have no relevant financial or non-financial interests to declare.

Author Contributions

Jorge Mario Herrera-Lopera: conceptualization (equal), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), writing – original draft (equal), writing – review and editing (equal). Carlos A. Cultid-Medina: conceptualization

(equal), formal analysis (equal), investigation (equal), methodology (equal), supervision (equal), writing – original draft (equal), writing – review and editing (equal).
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Supplementary Material
Holding the Line on Amphibian Conservation: Mapping Stable Priority Areas in
a Changing World

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Supplementary material 1: data cleaning, taxonomic updates, and gap-filling for functional and phylogenetic data

GBIF data records were cleaned using functions from the *scrubr* and *CoordinateCleaner* R packages (Chamberlain, 2022; Zizka et al., 2019) to filter erroneous coordinates, museum locations, and marine records. Only unique species-coordinate combinations were retained for analyses. Taxonomic updates and corrections were performed using the *AmphiNom* R package (Liedtke, 2019), based on the *Amphibian Species of the World 6.2* database from the American Museum of Natural History (Frost, 2024).

For functional data, continuous traits (body size and mass) were categorized into four groups based on quartiles, considering all species in the study area. This transformation ensured comparability across species while minimizing noise from continuous data variation. Furthermore, given that amphibian body size and mass may vary among populations, we consider that categorizing these traits provides a more reliable representation of each species' relative traits in comparison to others. Missing trait values were imputed using the mean or most frequent value within the species' genus (Fried et al., 2012; Gunton et al., 2011). While some studies suggest this approach is not the most robust (Taugourdeau et al., 2014), the large dataset and limited natural history information on species with missing data prevented the use of more refined methods, such as ecological or phylogenetic imputations (Moura et al., 2024; Taugourdeau et al., 2014).

For phylogenetic data, missing species in phylogeny were incorporated as sister groups (polytomies) within their genera, or family in case of monotypic genera (Fritz

and Rahbek, 2012). Species placement within the phylogeny was carried out using the *V.Phylomaker* package in R (Jin and Qian, 2022, 2019).

Supplementary Material 2: variable definitions and averaging protocols

Environmental variables used as predictors to estimate biodiversity metrics in this study. Climate variables were derived from the CHELSA database (Climatologies at High Resolution for the Earth's Land Surface Areas; <https://chelsa-climate.org/>), and elevation data were obtained from WorldClim (<https://www.worldclim.org/>). Geographical coordinates and distances were calculated from the centroids of hexagonal grid cells. Variable names correspond to standard bioclimatic codes and are provided with their respective units and data sources.

Code	Variable	Source	Units
bio1	mean annual air temperature	CHELSA	°C
bio2	mean diurnal air temperature range	CHELSA	°C
bio3	isothermality	CHELSA	%
bio4	temperature seasonality	CHELSA	%
bio5	mean daily maximum air temperature of the warmest month	CHELSA	°C
bio6	mean daily minimum air temperature of the coldest month	CHELSA	°C
bio7	annual range of air temperature	CHELSA	°C
bio8	mean daily mean air temperatures of the wettest quarter	CHELSA	°C
bio9	mean daily mean air temperatures of the driest quarter	CHELSA	°C
bio10	mean daily mean air temperatures of the warmest quarter	CHELSA	°C
bio11	mean daily mean air temperatures of the coldest quarter	CHELSA	°C
bio12	annual precipitation amount	CHELSA	mm
bio13	precipitation amount of the wettest month	CHELSA	mm
bio14	precipitation amount of the driest month	CHELSA	mm

bio15	precipitation seasonality	CHELSA	%
bio16	mean monthly precipitation amount of the wettest quarter	CHELSA	mm
bio17	mean monthly precipitation amount of the driest quarter	CHELSA	mm
bio18	mean monthly precipitation amount of the warmest quarter	CHELSA	mm
bio19	mean monthly precipitation amount of the coldest quarter	CHELSA	mm
npp	Net primary productivity	CHELSA	g C m ⁻² yr ⁻¹
x	Longitude	Hexagon centroid	Decimal degrees (WGS84)
y	Latitude	Hexagon centroid	Decimal degrees (WGS84)
elevation	Elevation in meters	WorldClim	meters
Distance	Geodesic distance, only for beta diversity models.	Coordinates distance	meters

Each realm was divided into hexagonal units (2° width; ~222.64 km at the equator).

CHELSA variables and WorldClim DEM have a resolution of 30 arc-seconds. Then, to match them with our response unit, we averaged the values of the cells within each hexagon, generating a single value per hexagon.

Supplementary Material 3: Scenario descriptions, GCM information, and processing steps

We used future climate projections based on the Shared Socioeconomic Pathways (SSPs), a set of five scenarios that describe alternative global futures combining socioeconomic trajectories with associated radiative forcing levels (O'Neill et al., 2017; Riahi et al., 2017). From these, we selected three that span the range of plausible climate outcomes by 2070-2100 available by CHELSA:

SSP1–2.6 (optimistic): low-emissions, sustainable development, strong mitigation (2.6 W/m²).

SSP3–7.0 (Moderate): intermediate scenario with regional rivalry, limited climate action (7.0 W/m²).

SSP5–8.5 (Pessimistic): high-emissions, fossil-fuel intensive, weak mitigation (8.5 W/m²).

For each climate scenario, we selected three Global Climate Models (GFDL-ESM4, UKESM1-0-LL, and MPI-ESM1-2-HR), which are recommended by CHELSA as the most reliable and broadly validated models within their CMIP6 ensemble (Karger et al., 2021).

We generated a single composite predictor set for each scenario by computing an unweighted average across these three GCMs, for each 2° width hexagon, across our extent.

Supplementary Material 4: Diversity measures

We quantified the three dimensions of alpha diversity: taxonomic, functional, and phylogenetic, using the Hill numbers framework (Chao et al., 2014; Hill, 1973; Jost, 2006). Because our estimates relied on GBIF occurrence records, which integrate data from a wide range of sources and therefore lack consistent abundance information (Lobo, 2008), we restricted our analyses to order-zero diversity ($q = 0$). This diversity order ignores abundance and effectively corresponds to species richness (${}^0\text{TD}$), richness of functional groups (${}^0\text{FD}$), or lineage richness (${}^0\text{PD}$), depending on the dimension considered (Chao et al., 2021).

Functional and phylogenetic diversities (${}^q\text{FD}$ and ${}^q\text{PD}$) require a quantitative value for each species within a sampling unit (Chao, 2024; Hsieh et al., 2016). To meet this requirement, each hexagonal grid cell was subdivided into smaller 0.2-degree sub-hexagons (≈ 22 km at the equator), from which we generated incidence matrices. These matrices served as proxies for abundance tables in subsequent calculations (Chao et al., 2021). Although this approach can introduce biases in metrics that depend on abundance, our use of order-zero diversity ensured that neither abundance nor incidence frequency influenced the results. All alpha diversity estimations were obtained using the iNEXT.3D package in R (Chao, 2024).

To evaluate beta diversity (taxonomic, functional, and phylogenetic), we applied the framework proposed by Cardoso et al. (2014), which generalizes the Jaccard index partitioning method (Carvalho et al., 2013) to incorporate functional traits and phylogenetic relationships. This approach produces three comparable metrics: taxonomic beta diversity ($T\beta$), functional beta diversity ($F\beta$), and phylogenetic beta

diversity ($P\beta$), all independent of abundance and therefore well suited for our dataset. Analyses were conducted separately for each biogeographic realm, generating pairwise distance matrices for each dimension. To capture overall dissimilarity, integrating both species turnover and richness variation, we used total beta diversity ($T\beta_{\text{total}}$, $F\beta_{\text{total}}$, and $P\beta_{\text{total}}$). All beta-diversity calculations were performed with the BAT package in R (Cardoso et al., 2014a).

Supplementary Material 5: Random forest models

To evaluate model performance, we first partitioned the data into an 85% training set and a 15% test set using a stratified procedure that preserved the distribution of diversity values, using the *Caret* R package (Kuhn, 2008, 2007). Model tuning focused on optimizing the *mtry* parameter, defined as the number of predictors randomly sampled at each tree split. We performed repeated cross-validation with 10 repeats while fixing the number of trees at 1000 and testing all possible *mtry* values from 1 to the total number of predictors (Breiman, 2001; Cutler et al., 2007; Probst et al., 2019). The optimal *mtry* was selected as the value maximizing the cross-validated coefficient of determination (R^2). The tuned model was then used to generate predictions for the independent test set, and predictive performance was quantified using the mean squared error (MSE) and R^2 calculated on these withheld data. We also assessed prediction accuracy visually through scatterplots comparing observed and predicted qTD values. Finally, using the optimal *mtry*, we fitted a final Random Forest model to the complete dataset (1000 trees) and quantified the contribution of each predictor to model performance based on the mean decrease in accuracy and the mean decrease in Gini impurity.

Supplementary Material 6: Model metrics

Variables definition are in Supplementary Material 2.

Alpha diversity models

Taxonomic alpha diversity ⁰ TD											
Realm	mtry	CV R2	CV RMSE	Test R2	Test RMSE	Predicted/observed correlation in test	Final model explained variance (%)	Final model RMSE	Predictor	%IncMSE	IncNodePurity
Afrotropic	1	0.54	15.89	0.44	12.01	0.68	45.11	15.77	x	13.68	8606.57
									y	20.23	7440.92
									bio13	17.02	11068.13
									bio15	17.96	8790.61
									bio18	23.33	11706.90
									bio19	17.35	10578.14
									bio3	12.34	6493.99
									bio8	16.12	7079.29
									elev	14.27	6819.61
Australasia	3	0.65	7.72	0.64	8.64	0.83	66.49	7.68	x	45.35	9660.45
									y	15.29	2688.21
									bio11	17.65	2513.91
									bio15	14.47	1930.42
									bio16	29.36	5904.06
									bio2	26.99	5244.10
									bio8	19.96	2818.44

									elev	17.62	4976.87
Indo-Malayan	4	0.41	11.50	0.29	13.52	0.58	35.13	11.81	x	27.16	4817.76
									y	16.44	2101.69
									bio1	10.06	1416.94
									bio13	5.14	1309.84
									bio17	12.82	1968.37
									bio18	9.65	1283.12
									bio2	18.62	3107.38
									bio3	9.88	1241.03
									bio8	10.44	2146.81
Nearctic	4	0.86	5.94	0.79	6.04	0.89	84.45	6.03	x	22.57	7686.44
									y	53.06	23324.36
									bio10	26.36	9583.23
									bio13	37.86	11092.43
									bio17	42.21	22037.31
									bio8	21.13	2623.89
									bio9	29.29	4191.34
									elev	21.59	3841.45
Neotropic	3	0.61	26.29	0.68	24.71	0.85	63.49	25.41	x	19.81	33281.52
									y	21.53	27895.03
									bio15	9.21	23336.86
									bio16	24.79	58572.93
									bio18	28.20	96312.22
									bio19	12.40	22701.30

										bio2	19.09	29199.29
										bio4	16.32	36070.12
										bio5	25.10	47593.86
										elev	29.48	62934.35
Palearctic	2	0.36	3.70	0.29	4.18		0.61	30.31	3.83	x	14.70	350.20
										y	12.90	251.86
										bio1	11.04	184.24
										bio13	16.08	337.28
										bio15	12.16	229.96
										bio19	4.42	180.25
										bio2	12.88	254.03
										bio3	13.69	218.82
										bio4	11.61	207.61
										bio8	14.04	240.85
										elev	5.80	233.27
										npp	13.52	298.93
Functional alpha diversity °FD												
Realm	mtry	CV R2	CV RMSE	Test R2	Test RMSE	Predicted/observed correlation in test	Final model explained variance (%)	Final model RMSE	Predictor	%IncMSE	IncNodePurity	
Afrotropic	2	0.60	1.93	0.64	2.74	0.82	54.87	3.67	x	17.38	488.84	
									y	22.11	516.19	
									bio13	26.23	884.84	
									bio15	19.93	594.77	
									bio18	29.84	1129.54	
									bio19	22.31	647.84	

										bio3	9.31	387.81
										bio8	16.39	357.92
										elev	15.53	405.42
Australasia	4	0.71	2.10	0.47	2.16		0.71	67.80	2.09	x	57.18	923.23
										y	18.00	217.83
										bio11	17.00	154.71
										bio15	12.45	117.25
										bio16	32.19	459.52
										bio2	29.79	392.13
										bio8	23.07	194.29
										elev	20.53	313.99
Indo-Malayan	7	0.44	3.46	0.52	3.18		0.78	42.35	3.43	x	43.43	656.25
										y	23.63	315.54
										bio1	10.82	92.29
										bio13	4.40	109.07
										bio17	11.56	116.23
										bio18	11.26	107.95
										bio2	15.30	234.43
										bio3	9.43	87.56
										bio8	9.98	149.44
Nearctic	4	0.80	1.78	0.90	1.33		0.95	82.22	1.69	x	25.33	475.24
										y	49.84	1401.99
										bio10	28.94	629.83
										bio13	41.70	1072.31

									bio17	36.13	1204.14
									bio8	27.09	289.44
									bio9	31.49	261.58
									elev	27.56	449.79
Neotropic	3	0.65	4.79	0.60	4.39	0.80	62.91	4.74	x	26.57	1322.88
									y	28.71	1247.29
									bio15	10.20	607.32
									bio16	33.57	2898.54
									bio18	31.42	2659.80
									bio19	15.88	793.04
									bio2	19.28	958.01
									bio4	23.99	1725.36
									bio5	23.81	1257.56
									elev	28.86	1517.20
Palearctic	2	0.42	1.25	0.58	1.19	0.85	43.88	1.22	x	17.78	41.52
									y	23.46	42.25
									bio1	12.37	21.95
									bio13	18.84	36.55
									bio15	13.54	28.83
									bio19	6.65	22.40
									bio2	19.84	38.49
									bio3	17.58	26.20
									bio4	13.90	25.74
									bio8	17.28	33.35

									elev	7.69	22.98
									npp	15.93	41.00
Phylogenetic alpha diversity ⁰ PD											
Realm	mtry	CV R ²	CV RMSE	Test R ²	Test RMSE	Predicted/observed correlation in test	Final model explained variance (%)	Final model RMSE	Predictor	%IncMSE	IncNodePurity
Afrotropic	2	0.53	1.78	0.48	1.63	0.72	50.99	1.75	x	21.04	137.54
									y	24.42	114.25
									bio13	24.00	183.63
									bio15	20.71	123.56
									bio18	27.52	196.00
									bio19	17.82	145.07
									bio3	13.75	75.73
									bio8	15.54	86.75
									elev	16.06	75.50
Australasia	2	0.65	0.68	0.61	0.79	0.84	65.95	0.68	x	32.60	53.99
									y	16.00	27.42
									bio11	18.22	24.28
									bio15	10.12	12.36
									bio16	25.91	50.11
									bio2	25.87	41.08
									bio8	17.76	23.31
									elev	17.93	40.36
Indo-Malayan	5	0.42	1.62	0.57	1.40	0.77	39.73	1.61	x	35.92	118.93
									y	15.26	41.88

										bio1	10.28	23.67
										bio13	3.48	19.41
										bio17	14.47	34.80
										bio18	8.27	25.77
										bio2	19.86	66.96
										bio3	11.67	24.02
										bio8	5.41	34.31
Nearctic	4	0.80	0.89	0.81	0.67	0.91	81.22	0.84		x	29.75	111.19
										y	50.56	279.48
										bio10	29.57	129.96
										bio13	44.22	277.43
										bio17	50.26	319.35
										bio8	22.68	45.16
										bio9	38.72	119.48
										elev	26.23	78.96
Neotropic	4	0.66	2.76	0.57	3.12	0.78	64.20	2.78		x	29.49	512.02
										y	26.26	357.22
										bio15	11.89	238.49
										bio16	30.43	839.43
										bio18	31.76	1152.08
										bio19	11.83	228.38
										bio2	19.95	315.67
										bio4	18.34	428.32
										bio5	23.81	531.11

										elev	28.75	681.11
Palearctic	3	0.35	0.91	0.46	0.78		0.78	35.00	0.76	x	25.59	20.64
										y	19.12	15.56
										bio1	11.29	10.13
										bio13	18.77	16.97
										bio15	14.78	13.89
										bio19	8.21	9.61
										bio2	19.44	18.78
										bio3	17.38	11.97
										bio4	14.99	12.41
										bio8	13.77	12.22
										elev	5.12	10.23
										npp	15.18	18.27

Beta models

The “d.” before each variable indicates difference (delta of pairwise sites).

Taxonomic beta diversity T β											
Realm	mtry	CV R ²	CV RMSE	Test R ²	Test RMSE	Predicted/observed correlation in test	Final model explained variance (%)	Final model RMSE	Predictor	%IncMSE	IncNodePurity
Afrotropic	4	0.83	0.05	0.82	0.05	0.91	83.50	0.05	d.geod	52.26	72.76
									d.bio13	18.07	32.75
									d.bio15	14.01	20.72

									d.bio18	19.15	30.37
									d.bio19	26.04	69.38
									d.bio3	13.78	23.27
									d.bio8	15.05	24.62
									d.elev	12.83	21.95
Australasia	2	0.83	0.06	0.82	0.07	0.91	82.74	0.06	d.geod	91.63	180.69
									d.bio11	25.31	52.17
									d.bio15	22.17	44.08
									d.bio16	25.16	50.38
									d.bio2	21.43	48.33
									d.bio8	33.48	58.52
									d.elev	19.85	46.32
Indo-Malayan	3	0.88	0.05	0.91	0.06	0.95	88.43	0.05	d.geod	30.54	22.31
									d.bio1	12.19	10.48
									d.bio13	11.80	10.97
									d.bio17	14.29	12.10
									d.bio18	12.52	11.80
									d.bio2	13.68	12.94
									d.bio3	14.61	14.09
									d.bio8	14.11	14.07
Nearctic	3	0.82	0.07	0.82	0.07	0.90	82.09	0.07	d.geod	213.65	805.67
									d.bio10	68.90	128.43
									d.bio13	73.26	186.61
									d.bio17	72.04	152.91

									d.bio8	55.58	94.79
									d.bio9	47.21	95.00
									d.elev	75.31	139.41
Neotropic	3	0.87	0.04	0.86	0.04	0.93	86.80	0.04	d.geod	55.50	125.05
									d.bio15	11.71	24.42
									d.bio16	12.74	26.07
									d.bio18	12.15	27.06
									d.bio19	17.22	57.17
									d.bio2	13.95	29.92
									d.bio4	16.06	28.67
									d.bio5	14.57	26.99
									d.elev	13.21	26.40
Palearctic	5	0.77	0.08	0.77	0.08	0.88	77.11	0.08	d.geod	116.36	154.35
									d.bio1	18.52	19.18
									d.bio13	19.80	19.03
									d.bio15	25.47	25.93
									d.bio19	16.14	17.36
									d.bio2	24.36	18.90
									d.bio3	18.92	19.37
									d.bio4	30.36	20.33
									d.bio8	17.44	17.41
									d.elev	20.33	17.52
									d.npp	19.43	17.50
Functional beta diversity F β											

Realm	mtry	CV R2	CV RMSE	Test R2	Test RMSE	Predicted/observed correlation in test	Final model explained variance (%)	Final model RMSE	Predictor	%IncMSE	IncNodePurity
Afrotropic	6	0.58	0.10	0.57	0.09	0.76	59.00	0.09	d.geod	117.90	134.51
									d.bio13	91.79	39.82
									d.bio15	59.40	27.85
									d.bio18	107.03	38.86
									d.bio19	60.67	59.27
									d.bio3	54.23	27.42
									d.bio8	42.94	34.56
									d.elev	48.21	26.79
Australasia	4	0.65	0.10	0.63	0.10	0.80	65.30	0.10	d.geod	158.98	205.61
									d.bio11	89.04	49.76
									d.bio15	74.23	51.67
									d.bio16	86.65	70.13
									d.bio2	84.30	81.15
									d.bio8	140.27	71.32
									d.elev	55.84	64.53
Indo-Malayan	7	0.68	0.09	0.6176531v	0.09	0.79	67.13	0.09	d.geod	73.94	39.11
									d.bio1	16.59	9.19
									d.bio13	13.16	9.49
									d.bio17	21.07	11.11
									d.bio18	17.44	11.66
									d.bio2	15.43	9.73
									d.bio3	18.95	10.28

									d.bio8	20.48	12.43
Nearctic	5	0.73	0.08	0.72	0.08	0.85	73.55	0.08	d.geod	413.20	754.63
									d.bio10	195.66	141.40
									d.bio13	191.47	185.07
									d.bio17	238.12	107.05
									d.bio8	224.56	92.58
									d.bio9	199.98	96.86
									d.elev	223.74	154.79
Neotropic	5	0.62	0.08	0.61	0.08	0.78	62.21	0.08	d.geod	111.29	192.76
									d.bio15	33.78	35.61
									d.bio16	38.85	39.01
									d.bio18	24.23	35.02
									d.bio19	32.19	63.42
									d.bio2	36.78	38.84
									d.bio4	57.29	58.01
									d.bio5	40.92	40.85
									d.elev	31.84	37.74
Palearctic	8	0.63	0.10	0.63	0.11	0.80	63.58	0.10	d.geod	179.92	151.90
									d.bio1	49.43	16.32
									d.bio13	65.27	16.68
									d.bio15	57.74	24.41
									d.bio19	36.12	17.42
									d.bio2	57.54	32.79
									d.bio3	66.55	18.64

									d.bio4	77.01	16.41
									d.bio8	44.70	14.08
									d.elev	45.06	20.21
									d.npp	39.06	15.55
Phylogenetic beta diversity Pβ											
Realm	mtry	CV R ²	CV RMSE	Test R ²	Test RMSE	Predicted/observed correlation in test	Final model explained variance (%)	Final model RMSE	Predictor	%IncMSE	IncNodePurity
Afrotropic	8	0.71	0.08	0.67	0.08	0.82	71.26	0.08	d.geod	209.25	136.41
									d.bio13	131.83	28.43
									d.bio15	73.37	21.67
									d.bio18	306.84	68.58
									d.bio19	90.37	69.25
									d.bio3	58.07	18.81
									d.bio8	51.03	18.30
									d.elev	50.91	18.87
Australasia	4	0.82	0.08	0.82	0.08	0.90	82.53	0.07	d.geod	228.88	222.30
									d.bio11	101.18	41.80
									d.bio15	170.96	42.61
									d.bio16	232.76	192.06
									d.bio2	188.58	78.51
									d.bio8	220.20	61.80
									d.elev	141.77	51.72
Indo-Malayan	4	0.71	0.08	0.72	0.07	0.85	71.67	0.07	d.geod	64.33	35.44
									d.bio1	17.23	7.42

									d.bio13	12.08	6.85
									d.bio17	22.33	8.76
									d.bio18	14.29	6.86
									d.bio2	16.11	8.07
									d.bio3	15.70	7.33
									d.bio8	16.24	8.60
Nearctic	4	0.70	0.09	0.70	0.09	0.84	70.93	0.09	d.geod	390.49	678.50
									d.bio10	206.85	143.54
									d.bio13	299.71	192.22
									d.bio17	355.91	275.96
									d.bio8	266.00	116.15
									d.bio9	316.84	122.29
									d.elev	297.88	126.06
Neotropic	5	0.71	0.07	0.73	0.06	0.86	71.71	0.06	d.geod	147.64	211.01
									d.bio15	24.20	25.72
									d.bio16	37.39	27.58
									d.bio18	40.80	32.14
									d.bio19	27.87	54.54
									d.bio2	34.07	25.67
									d.bio4	55.12	34.17
									d.bio5	42.36	29.74
									d.elev	48.17	34.78
Palearctic	6	0.63	0.10	0.64	0.10	0.80	64.12	0.10	d.geod	210.40	122.10
									d.bio1	62.32	13.38

d.bio13	70.17	18.57
d.bio15	59.37	25.96
d.bio19	52.31	14.20
d.bio2	55.86	21.47
d.bio3	65.80	16.69
d.bio4	60.68	26.54
d.bio8	40.56	13.21
d.elev	68.50	21.13
d.npp	83.38	19.31

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Conclusões gerais

Para desenvolver estratégias realmente eficazes de conservação de anfíbios em escala global, é fundamental enfrentar, antes de tudo, as lacunas de informação e os vieses de conhecimento existentes sobre a distribuição do grupo. No capítulo 1, demonstramos que os dados disponíveis globalmente são amplamente incompletos, com níveis de viés que variam entre os diferentes domínios biogeográficos. Assim, parte dos recursos destinados à conservação de anfíbios deve ser direcionada à redução dessas lacunas, ampliando o esforço de amostragem e a coleta de dados, especialmente nas regiões tropicais e na porção asiática do Paleártico, que contem a maioria das áreas subamostradas.

Com os dados atualmente disponíveis é possível identificar as principais regiões que concentram a maior diversidade de anfíbios em cada domínio biogeográfico. Essas áreas, que deveriam ser tratadas como prioritárias na formulação inicial de estratégias de conservação de habitats de anfíbios, correspondem em grande medida aos *hotspots* já reconhecidos, além de incluir novos *hotspots* revelados pela incorporação de dimensões de diversidade além da taxonômica (capítulo 2). A maior parte dessas regiões permanece estável sob cenários climáticos futuros (capítulo 3), o que reforça seu potencial como referências estratégicas para orientar investimentos na redução de lacunas de informação e na avaliação do fortalecimento e da interconexão das áreas protegidas no presente, garantindo assim a conservação também no futuro.

As abordagens e os resultados apresentados neste trabalho têm, como principal limitação, a escala espacial empregada. Devido às exigências logísticas de uma análise global, trabalhamos com um grão espacial relativamente amplo, o que reduz a aplicabilidade direta dos resultados. Ainda assim, esperamos que tanto nossas

análises quanto a metodologia e os protocolos delineados ao longo dos três capítulos possam servir de base e inspiração para investigações em escalas mais refinadas, capazes de gerar recomendações com aplicação prática mais imediata.

As áreas protegidas atualmente existentes já desempenham um papel essencial na conservação da biodiversidade de anfíbios. Elas protegem, e continuarão protegendo no futuro, uma parcela significativa das regiões com maior diversidade multidimensional do grupo. Por isso, é fundamental que, alinhadas aos acordos internacionais, essas áreas sejam fortalecidas e conectadas entre si, de forma a ampliar sua efetividade e assegurar, no médio e longo prazo, sua função como refúgios para os anfíbios.

Este trabalho também abre um conjunto de questões que merecem ser exploradas nos próximos anos, para diferentes escalas espaciais, temporais e taxonômicas. Entre elas estão: como a diversidade multidimensional de anfíbios pode mudar à medida que reduzimos os vazios e vieses de amostragem? Quais regiões com lacunas de informação permanecem preservadas o suficiente para serem exploradas e potencialmente revelar diversidade ainda desconhecida? Nas áreas de maior diversidade, quais seriam as rotas de menor custo para interligar áreas protegidas, formando corredores realmente funcionais para as populações de anfíbios? Quais os custos econômicos de conservar essas áreas, em comparação com os benefícios proporcionados pelos serviços ecossistêmicos que os anfíbios oferecem? E, ainda, quais matrizes de uso do solo são simultaneamente viáveis economicamente e favoráveis à conectividade entre os anfíbios das áreas protegidas? Estas e muitas outras perguntas são aquelas que esperamos que este trabalho motive e ajude a impulsionar.