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TESIS DOCTORAL

Las comunidades de anfibios en los bosques Neotropicales estacionalmente secos

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CERTIFICAN:

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral: **“Las comunidades de anfibios en los bosques estacionalmente secos del Neotrópico”**, han sido realizados bajo su supervisión y son aptos para ser presentados por el ingeniero Diego Armijos Ojeda ante el tribunal que en su día se consigne, para aspirar al Grado de Doctor en el Programa de Doctorado en Conservación de Recursos Naturales por la Universidad Rey Juan Carlos.

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DEDICATORIA

Este trabajo está dedicado con infinito cariño para toda la gente que vive en los bosques secos y a quienes los protegen cada día.

Que todos los esfuerzos que dedicamos para la conservación de este maravilloso ecosistema, sirvan a los diferentes actores, para construir estrategias que permitan a las futuras generaciones seguir disfrutando de los saltos de las ranas y de sus hermosos cantos, que anuncian en coro, la llegada del tan esperado invierno.

Engystomops montubio
Rana túngara montubia

Noemi Cevallos ©Picturatus

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Trachycephalus jordani
Rana de Casco de Jordan

Santiago Cordero © Picturatus

RESUMEN

Antecedentes

Los bosques estacionalmente secos del Neotrópico se distribuyen en parches desde el norte de Argentina hasta el noroeste de México. A pesar de que albergan una interesante riqueza biológica, han recibido poca atención científica en comparación con los estudios llevados a cabo en bosques lluviosos tropicales. Esta situación es más preocupante en el caso de los anfibios, donde el conocimiento es preliminar e insuficiente. Si bien el Neotrópico en general, tiene una alta diversidad de anfibios, muy pocas de esas especies están adaptadas a los ecosistemas secos.

Los periodos de sequía en estos ecosistemas de más de seis meses por año, presentan serias limitaciones ecológicas para los anfibios, que son organismos susceptibles a la desecación. Sin embargo, las adaptaciones que poseen para sobrevivir a la escasez de agua y alimento, las convierten en especies únicas. En este contexto, es necesario comprender cuales son los factores que determinan los patrones de diversidad de anfibios de bosques secos tanto a escala del Neotrópico como a escalas más específicas. Esta información se constituye en información base fundamental para establecer medidas de manejo y conservación de este importante grupo a nivel regional.

En el neotrópico, los ecosistemas estacionalmente secos enfrentan altos niveles de deforestación, un acelerado cambio de uso de suelo y una perturbación crónica que afecta incluso a bosques naturales. Se han acumulado muchas evidencias que muestran el fuerte impacto que tiene el cambio de uso del suelo y la deforestación en ecosistemas secos sobre los anfibios, sobre todo en la abundancia de las especies, diversidad taxonómica y diversidad funcional. Además, los anfibios son especialmente sensibles a cambios tanto en las condiciones microclimáticas y al calentamiento global.

El presente trabajo es un intento para mejorar el conocimiento sobre la diversidad y distribución de los anfibios de los bosques Neotropicales estacionalmente secos y aportar información crítica para la conservación de este importante grupo taxonómico. La apremiante necesidad de completar la información disponible cuando la destrucción y degradación de estos bosques es enorme, hace prioritario nuestro esfuerzo.

Objetivos

Se plantearon tres objetivos para el desarrollo de la tesis doctoral:

- Analizar los factores que determinan los patrones de diversidad y endemicidad de los anfibios del bosque Neotropical estacionalmente seco y de la región Pacífico Ecuatorial (Región Tumbesina).
- Determinar la vulnerabilidad de las especies de anfibios y de los núcleos biogeográficos de bosque Neotropical estacionalmente seco al cambio climático y a la deforestación.
- Identificar las áreas prioritarias para la conservación de la diversidad de anfibios en el bosque seco de la región Pacífico Ecuatorial (Región Tumbesina).

Metodología

Como base para el desarrollo del trabajo doctoral se construyó una base de datos con más de 40.000 registros de anfibios en los bosques estacionalmente seco del Neotrópico, que fueron obtenidos a partir de revisión de literatura científca, bases de datos y registros de campo. Esta base nos permitió articular un análisis de los patrones de distribución de las especies de bosque seco a la escala Neotropical y también a la escala de la región Pacífico Ecuatorial (Región Tumbesina).

Para evaluar la vulnerabilidad al cambio climático de los anfibios del bosque seco neotropical se modelaron las condiciones futuras, considerando tres modelos de circulación global, cada uno bajo dos escenarios de Rutas de Concentración Representativa (RCP) para la concentración de gases de efecto invernadero: RCP 4.5 y RCP 8.5 (período 2041-2060). Evaluamos los patrones generales de cambio en altitud y direccionalidad entre las áreas actuales y proyectadas adecuadas para cada especie, así como los cambios en el hábitat disponible, analizamos los cambios en la idoneidad del área y finalmente evaluamos la vulnerabilidad de las especies al cambio climático.

Finalmente, propusimos identificar zonas prioritarias para la conservación de anfibios dentro de la region Pacífico Ecuatorial (Región Tumbesina), basándose en la distribución potencial de todas las especies de anfibios conocidas que se encuentran allí. Generamos un índice de prioridad unificando datos sobre la riqueza de especies, endemismo y estado de conservación, clasificando toda el área de SDF ecuatorial en prioridad alta, media o baja para la conservación de anfibios; además, evaluamos el estado actual de protección y la cobertura/uso del suelo para cada nivel de prioridad.

Resultados

Cap I: Reportamos el impresionante valor de 260 especies de anfibios para los bosques estacionalmente secos del Neotrópico, de las cuáles 135 son endémicas de este ecosistema. Encontramos que tanto la temperatura como la precipitación, desempeñaron un papel crítico como impulsores positivos de la riqueza de anfibios, y las subregiones con áreas más grandes mostraron una mayor riqueza total. Aunque las subregiones vecinas tendieron a compartir más especies, la rotación entre áreas fue alta. El endemismo en general es alto, pero no mostró ninguna relación con la extensión de las subregiones.

Cap II: En la región Pacífico Ecuatorial (Región Tumbesina), el conjunto de datos final incluyó 2,032 registros de ocurrencia para 30 especies de anfibios, pertenecientes a ocho familias de anuros. Además, se proporcionan datos sobre el estado de conservación, uso del hábitat, sitio de deposición de huevos, modo reproductivo y tamaño corporal, junto con una clave de identificación para todas las especies encontradas. Los resultados indican un fuerte sesgo de muestreo con un déficit en la parte peruana del área de estudio y una necesidad urgente de inventarios dirigidos a áreas submuestreadas, utilizando métodos taxonómicos modernos.

Cap III: La expansión del rango de distribución de las especies ocurrirá bajo ambos escenarios futuros de cambio climático. Los nuevos hábitats adecuados se ubicarán en elevaciones más altas y mantendrán una extension similar a la que tienen actualmente. Encontramos valores de vulnerabilidad inferiores a 0.5 para la mayoría de las especies. Solo cuatro especies demostraron alta vulnerabilidad en ambos escenarios RCP. El Chaco Seco, el bosque Chiquitano y los bosques de México y Centroamérica fueron los núcleos con mayor vulnerabilidad promedio al cambio climático.

Cap IV: En la región Pacífico Ecuatorial (Región Tumbesina), menos de una cuarta parte de las áreas de prioridad alta y media carecen actualmente de cualquier forma de protección, y que casi la mitad de las áreas de alta prioridad se encuentran en sitios muy perturbados. El hecho de que áreas importantes en niveles de prioridad media y alta aún alberguen vegetación natural enfatiza la oportunidad para la conservación si se toman acciones inmediatas para expandir la red de áreas protegidas, enfocándose en comunidades más diversas y endémicas y creando corredores biológicos.

Conclusiones

A pesar de las limitaciones ecológicas que representan los bosques secos Neotropicales, albergan una importante riqueza de anfibios, con alto nivel de endemismo. Existen regiones como los bosques secos de Centroamérica donde el endemismo puede llegar al 82% de las especies. Además, se estudió a detalle la región Pacífico Ecuatorial, que incluye 30 especies de anfibios de las cuáles la tercera parte, son endémicas del ecosistema. Se han identificado también zonas con vacíos de conocimiento donde es necesario priorizar los esfuerzos de investigación.

La diversidad de anfibios de las diferentes regiones de bosque seco Neotropical está determinada principalmente por la disponibilidad de agua y temperatura, que fueron predictores importantes de la riqueza. Además, la conectividad y el tamaño de las subregiones influyen positivamente en el número de especies presentes en cada una de las subregiones estudiadas. El área de las regiones influye en la riqueza específica pero no está relacionada con el porcentaje de endemismo que se encontró en cada una. En lo que corresponde a la región Pacífico Ecuatorial la mayor riqueza se concentró hacia el centro y norte de la región, la baja riqueza hacia el sur está asociada a las condiciones climáticas que determina la cercanía al desierto de Sechura.

La mayoría de especies de anfibios muestran una vulnerabilidad media o baja al cambio climático, ya que ampliarían su área de distribución geográfica, hay que considerar que el potencial de estas especies para colonizar nuevas áreas es complejo, ya que depende de la disponibilidad de hábitats adecuados, la competencia interespecífica y su capacidad de dispersión. Por ello, las estrategias de conservación no deben centrarse solo en las distribuciones actuales y futuras, sino que deben considerar temas como la calidad del hábitat remanente y la historia natural de las especies, que puede incluir una variedad de rasgos funcionales, tal como lo hemos observado para la región Pacífico Ecuatorial.

Los esfuerzos actuales de conservación de anfibios en la región Pacífico Ecuatorial son insuficientes y existen vacios importantes en lo que se refiere a la efectividad de las áreas protegidas. Las estrategias de conservación deberían centrarse en ampliar los sistemas de áreas protegidas y garantizar la conectividad entre los remanentes de bosques, considerando tanto las reservas gubernamentales como las privadas y comunitarias.

ABSTRACT

Background

The Neotropical seasonally dry forests are distributed in patches from northern Argentina to northwestern Mexico. Although they are home to a remarkable biological richness, they have received little scientific attention compared to rainforests. The situation is more evident in the case of amphibians, where knowledge is preliminary and insufficient. Although overall there is a high diversity of amphibians in the Neotropics, very few of these species are adapted to dry ecosystems.

These ecosystems are characterized by dry seasons lasting more than six months per year, this representing a serious ecological limitation for amphibians, which are susceptible to desiccation. As a result, the amphibians that survive here possess unique adaptations to resist water and food scarcity. In this context, it is necessary to understand the factors that determine the diversity of dry forest amphibians, at both Neotropical and regional scale. This information constitutes a fundamental basis for establishing management and conservation measures for this important group.

In the neotropics, the seasonally dry ecosystems face high rates of deforestation, accelerated land use change, and a chronic disturbance that affects even natural forests. Land-use change and deforestation have a strong impact on amphibians, reducing species abundance, taxonomic diversity, and functional diversity. In addition, amphibians are especially sensitive to changes in both microclimatic conditions and global warming.

The present work aims to improve knowledge on the diversity and distribution of amphibians in the Neotropical seasonally dry forests and to provide critical information for the conservation of this important taxonomic group. In the context of the enormous destruction and degradation of these forests, there is a pressing need for updated information regarding its threatened biodiversity, making our efforts a priority.

Objectives

This doctoral thesis has three main objectives:

- To determine the factors influencing the diversity and endemicity patterns of the amphibians inhabiting the Neotropical seasonally dry forest in general, and the Equatorial Pacific region (i.e., the Tumbesian region).
- To examine how vulnerable the endemic amphibians from different Neotropical seasonally dry forest regions are to climate change and deforestation.
- To identify the priority areas for the conservation of amphibian diversity in the dry forests of the Equatorial Pacific region (Tumbesian region).

Methodology

For the analysis, we generated a database with more than 40,000 records of amphibians from the Neotropical seasonally dry forests, obtained from a review of scientific literature, databases and field records. This database allowed us to analyze the distribution patterns of dry forest species at the scale of the whole Neotropicals, and also at the scale of the Equatorial Pacific region.

To assess the vulnerability to climate change of Neotropical dry forest amphibians, we modeled future conditions, considering three global circulation models, each under two Representative Concentration Pathways (RCP) scenarios for greenhouse gas concentration: RCP 4.5 and RCP 8.5 (period 2041-2060). We assessed general patterns of change in altitude and direction between current and projected suitable areas for each species, as well as changes in available habitat, analyzed changes in area suitability, and finally assessed species vulnerability to climate change.

Finally, we aimed to identify the priority zones for amphibian conservation within the Equatorial Pacific region, based on the potential distribution of all amphibian species known to occur there. We generated a priority index unifying data on species richness, endemism and conservation status, classifying the entire Equatorial Pacific area into high, medium or low priority for amphibian conservation; in addition, we determined the current protection status and land cover/land use for each priority level.

Results

Chapter I: We report an impressive amphibian richness for the Neotropical seasonally dry forests, consisting of 260 species, of which 135 are endemic to this ecosystem. We found that both temperature and precipitation played a critical role as positive drivers of amphibian richness, and subregions with larger areas showed higher total richness. Although subregions that were closer to each other tended to share more species, turnover rates were high. Overall, endemism is high and in most cases is associated with the isolation between the subregions.

Chapter II: In the Equatorial Pacific region (Tumbesian Region), the final dataset included 2,032 occurrence records for 30 species of amphibians, belonging to eight families of anurans. In addition, data on conservation status, habitat use, egg deposition site, reproductive mode and body size are provided, along with an identification key for all species encountered. The results indicate a strong sampling bias, deficient in the Peruvian part of the study area, as well as an urgent need for targeted inventories in sub-sampled areas, using modern taxonomic methods.

Chapter III: The two future climate change scenarios predict an expansion of the distribution range for most of the dry forest species. This expansion occurs mostly towards areas with higher elevation, and frequently towards natural habitat. We found that dry forest species have a low vulnerability (below 0.5), only four species showing a high vulnerability under both RCP scenarios (4.5 and 8.5). The Dry Chaco, the Chiquitano forests and the dry forests of Mexico and Central America were the regions with the highest average vulnerability to climate change.

Chapter IV: In the Equatorial Pacific region (Tumbesian Region), less than a quarter of the high and medium priority areas currently lack any form of protection, and almost half of the high priority areas are in highly disturbed sites. The fact that important areas at medium and high priority levels still harbor natural vegetation emphasizes the opportunity for conservation if immediate action is taken to expand the protected area network, focusing on more diverse and endemic communities and creating biological corridors.

Conclusions

Despite the ecological limitations inherent to the Neotropical seasonally dry forests, an important richness of amphibians lives here. Overall, 39% of the species are endemic to this type of ecosystem, and the level of species which are unique to each of the regions varied between 16% and 63%.

Amphibian diversity in the different regions of the Neotropical seasonally dry forest is mainly determined by water availability and temperature. Additionally, greater connectivity and greater size of the subregions have a positive influence on the number of species present in each of the subregions studied. In the Equatorial Pacific region, the greatest richness was concentrated towards the center and north of the region, with a lower diversity towards the south, determined by more extreme climatic conditions close to the Sechura desert.

Most amphibian species show a medium or low vulnerability to climate change; however, there are other pressures that represent a more important risk for the survival of these species. At the scale of the Equatorial Pacific region, large extensions of the high priority areas for the conservation of amphibians are not protected and there are significant gaps in the effectiveness of protected areas. Conservation strategies should focus on expanding protected area systems and ensuring connectivity between forest remnants, that include governmental, private and community reserves.

INTRODUCCIÓN

En el Neotrópico, los bosques estacionalmente secos se distribuyen latitudinalmente en parches ubicados en distintas zonas desde el norte de Argentina hasta el noroeste de México (Linares-Palomino et al. 2011). A pesar de que estos ecosistemas secos ocupan el 42% de la superficie de los bosques tropicales a nivel global y albergan una interesante riqueza biológica, han recibido poca atención científica en comparación con los estudios llevados a cabo en bosques lluviosos tropicales (Espinosa et al. 2012). Esta situación es más preocupante en el caso de los anfibios, donde el conocimiento es preliminar y aún muy insuficiente (Székely et al. 2016). Varios factores influyen en esta falta de información, incluido el sesgo causado por la preferencia de los investigadores a los bosques tropicales húmedos y nubosos y las limitaciones logísticas impuestas por la accesibilidad en el periodo invernal (época de lluvias), cuando los anfibios están activos y pueden ser detectados.

Figura 1. Estacionalidad del bosque seco y cambios de la vegetación, observados en un mismo punto, en la Reserva Ecológica Arenillas (Ecuador).

Si bien el Neotrópico en general, tiene una alta diversidad de anfibios, con un 38% de las especies conocidas a nivel global (Bolaños et al. 2008), muy pocas de esas especies están adaptadas a los ecosistemas secos. Esto hace que existan fuertes diferencias entre la riqueza de anfibios en un bosque húmedo y un bosque estacionalmente seco (Calvo-Alvarado et al. 2013). Los periodos de sequía en estos ecosistemas, los cuales pueden durar más de seis meses al año, presentan serias limitaciones ecológicas a los diferentes grupos taxonómicos (Maass y Burgos 2011), en especial a los anfibios, ya que son organismos especialmente susceptibles a la desecación (Duellman y Trueb 1994). Sin embargo, las adaptaciones que han generado las especies de anfibios para sobrevivir a la escasez de agua y alimento que se presenta durante el periodo seco (Ceballos, 1995; Stoner y Timm 2011; Chazdon et al. 2011) los convierten en especies únicas, pues cada una tiene una historia natural específica adaptada a una estacionalidad climática bien marcada (Székely et al. 2016).

Figura 2. Anfibios que mueren por desecación en el bosque seco.

Figura 3. Adaptaciones de los anfibios de bosque seco. A la izquierda se observa un nido de espuma que ayuda a mantener la humedad por largos periodos de tiempo. A la derecha, se observa una especie que se entierra encapsulada para resistir los meses sin lluvia.

Lamentablemente, conocemos muy poco en el Neotrópico de los procesos de ensamblaje de comunidades de los anfibios e incluso, para amplias regiones, no se sabe ni la diversidad total de las especies que atesoran estas regiones. En este contexto, es necesario comprender cuales son los factores que determinan los patrones de diversidad de anfibios de bosques secos tanto a escala del Neotrópico (Cápitulo I) como a escala más específica como la Pacífico Ecuatorial, que corresponde a las zonas de bosque estacionalmente seco de la Región Tumbesina (Capitulo II). Esta información se constituye en información base fundamental para establecer medidas de manejo y conservación de este importante grupo a nivel regional.

Si bien los bosques secos son biológicamente menos diversos que los bosques lluviosos, la importancia de estos bosques radica en el alto endemismo que poseen manteniendo una diversidad nada despreciable, por ejemplo, en la región Pacífico Ecuatorial se consideran endémicas el 21% de las especies de árboles, el 24% de las aves y el 25% de los anfibios (Escribano et al. 2017). Lastimosamente, esta singular diversidad se está perdiendo, factores como la deforestación y la degradación de bosques a los que esta sometido este ecosistema lo ha posicionado como un ecosistema prioritario para la conservación (Beuchle et al. 2015; Cadavid-Florez et al. 2019; Jara-Guerrero et al. 2021). En el neotrópico estos ecosistemas enfrentan altos niveles de deforestación y cambio de uso de suelo, en centro América ha desaparecido el 66% del bosque seco natural y en América del sur se ha perdido más del 60% (Portillo-Quintero y Sánchez-Azofeifa 2010). Se han acumulado muchas evidencias que muestran el fuerte impacto que tiene el cambio de uso del suelo en ecosistemas secos sobre los anfibios, sobre todo en la abundancia de las especies, diversidad taxonómica y diversidad funcional (Sung et al. 2012; Fraga Ramirez et al. 2017; Crane et al. 2018).

Figura 4. Deforestación y cambio de uso de suelo en el bosque seco.

Aunque la deforestación directa sigue siendo el factor de destrucción más importante, la pérdida de cobertura de bosque como consecuencia de una perturbación multidimensional crónica, es si cabe, más perturbador para la diversidad de estos bosques. Varios estudios han mostrado, por ejemplo, que el disturbio crónico reduce la diversidad de árboles (Jara-Guerrero et al. 2021), murciélagos (Valle et al. 2021). Aparentemente la pérdida de diversidad estaría mediada por cambios estructurales en la vegetación (Jara-Guerrero et al. 2021) lo cual incrementa la exposición a la radiación y produce un aumento del estrés hídrico para la mayor parte de sus organismos. Los anfibios son especialmente sensibles a cambios tanto en las condiciones microclimáticas (Hartwell y Ollivier 1998), como al calentamiento global (Blaustein et al. 2003) ya que son vulnerables a los cambios de temperatura y precipitación (Cayuela et al. 2012; Kiesecker et al. 2001; Lawler et al. 2010). Para ello es importante entender el efecto que puede tener el cambio climático sobre las comunidades de anfibios de los bosques secos Neotropicales (Capítulo III).

A pesar de la situación actual de los bosques secos, sus amenazas y la importancia que tienen para la conservación, las áreas protegidas cubren menos del 5% de la superficie original del ecosistema (Portillo-Quintero y Sánchez-Azofeifa 2010). Por otro lado, es conocido que las áras protegidas son una de las formas más comunes y eficientes de garantizar la existencia a largo plazo de las especies, especialmente para los anfibios (Watson et al. 2014; Gray et al. 2016; Pacifici et al. 2020; Halstead et al. 2022). Sin embargo, no está clara la efectividad de estas áreas para cubrir la distribución de anfibios en los bosques secos (Fajardo et al. 2023) y qué sitios adicionales representarían una prioridad para optimizar los esfuerzos de conservación de este grupo, para ello, es necesario empezar a evaluar la efectividad de las áreas protegidas para la conservación de anfibios en las diferentes regiones de bosque seco (Capítulo IV).

El presente trabajo es un intento para mejorar el conocimiento sobre la diversidad y distribución de los anfibios de los bosques Neotropicales estacionalmente secos y aportar información crítica para la conservación de este importante grupo taxonómico. La apremiante necesidad de completar la información disponible cuando la destrucción y degradación de estos bosques es enorme, hace prioritario nuestro esfuerzo. Por otro lado, comprender las funciones ecológicas que los anfibios desarrollan en los bosques estacionales, así como las estrategias de adaptación son información básica para desarrollar programas de conservación realistas para preservar los anfibios y, sobre todo, estos ecosistemas únicos y los servicios ambientales que brindan.

Figura 5. Paisaje de un bosque seco en época invernal.

OBJETIVOS ESPECÍFICOS

Los objetivos específicos que se han abordado en esta tesis doctoral son:

- Analizar los factores que determinan los patrones de diversidad y endemicidad de los anfibios del bosque Neotropical estacionalmente seco y de la región Pacífico Ecuatorial.
  Este objetivo se ha desarrollado en dos capítulos:
  I. *Patterns of diversity in amphibians of the Neotropical Seasonally Dry Forests*
  II. *Amphibians of the Equatorial Seasonally Dry Forest of Ecuador and Peru*

- Determinar la vulnerabilidad de las especies de anfibios y de los núcleos biogeográficos de bosque Neotropical estacionalmente seco al cambio climático y a la deforestación.
  Este objetivo se ha desarrollado en el siguiente capítulo:
  III. *Climate change and distribution expansion of dry forest endemic amphibians: a threat to biological diversity?*

- Identificar las áreas prioritarias para la conservación de la diversidad de anfibios en el bosque seco de la región Pacífico Ecuatorial (Región Tumbesina).
  Este objetivo se ha desarrollado en el siguiente capítulo:
  IV. *Priority areas for amphibian conservation in Ecuadorian Pacífic region*

Engystomops montubio
Rana túngara montubia

Noemi Cevallos ©Picturatus

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CAPÍTULO I

Patterns of diversity in amphibians of the Neotropical Seasonally Dry Forests

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Abstract

The Neotropical Seasonally Dry Forests (NSDFs) are amongst the most vulnerable biomes worldwide, due to their fragility, high diversity and anthropic pressure, but also amongst the most poorly studied. Because of the extended dry season and stressful climate, they seem as an unlikely habitat for amphibians. Consequently, studies centered on this group are scarce and information on their diversity and biogeography at continental scale is currently lacking. However, NSDFs are home to an outstanding amphibian diversity with an impacting variety of ecophysiological and life-history adaptations. Here we compile the available records of amphibians in the NSDFs to understand their distribution patterns and historical relationships between NSDF dominated regions. We reported the impressive value of 260 amphibian species for the NSDFs. We found that both temperature and precipitation (their annual mean and the variation amplitude) had a critical role as positive drivers of amphibian assemblages, and subregions with larger areas showed a higher total richness. Although neighboring subregions tended to share more species, the turnover between areas was high, with only few species present in several subregions. This emphasizes the uniqueness of each subregion, a feature that highlights the necessity for developing conservation measures at such subregion scale. Although the Dry Chaco and the Mexican and Central American Dry Forests showed a high diversity, smaller subregions, especially those from the Pacific coast of Ecuador and Peru, reached high levels of diversity and endemism, highlighting the need to preserve threatened assemblages and intensify focused research.

Key words: Anurans, communities, dry ecosystems, frogs, toads.

Introduction

Humans are responsible for the dramatic species extinction and decline rates occurring in recent times, caused mostly through land-use change, although global warming is sharply scaling up these effects (Guo et al. 2018, Turvey & Crees 2019). The Neotropics host the highest species richness for various taxonomic groups (Antonelli & Sanmartin 2011, Jenkins et al. 2013a, b, Ulloa Ulloa et al. 2017, Raven et al. 2020), also harboring several global hotspots of biodiversity (Myers et al. 2000). Unfortunately, this is accompanied by its accelerated demise (Betts et al. 2017, Burbano-Girón et al. 2022). It is well-known that Latin America is among those regions experiencing a higher biodiversity loss (Antonelli 2022). Its generalized decline of diversity seems to be especially exacerbated in the case of amphibians (Wanger et al. 2010, Harfoot et al. 2021, Capdevila et al. 2022), probably because they are highly dependent on water (Lips et al. 2005) and are disproportionately affected by habitat loss and fragmentation (Cordier et al. 2021). As a consequence, amphibians are dramatically threatened in the Neotropics which houses almost half of the total number of amphibian species known globally (Bolaños et al. 2008). Unfortunately, this critical situation mirrors what occurs for amphibians at the global scale (Catenazzi 2015).

Neotropical Seasonally Dry Forests (hereafter NSDFs) are widely distributed from northern Argentina to northwestern Mexico (Linares-Palomino et al. 2011). Although NSDFs occupy 42% of the total area of neotropical forests, harbor interesting biological diversity and are highly threatened (Pennington et al. 2009), they have received little scientific attention compared to the effort devoted to tropical rainforests (Espinosa et al. 2012, Sánchez-Azofeifa et al. 2005). Land use changes, direct deforestation and habitat fragmentation are accelerating their biodiversity loss (Beuchle et al. 2015, Manchego et al. 2017, Cadavid-Florez et al. 2019, Jara-Guerrero et al. 2021, Valle et al. 2021).

The most significant ecological feature of NSDFs is the existence of a dry season lasting for at least three months annually (Maass & Burgos 2011), which limits the performance and survival of amphibians, sorting the species through trait selection (Shoemaker 1988). This has a homogenizing effect on amphibian assemblages, reducing amphibian richness in drylands (including NSDFs) compared to humid habitats (Calvo-Alvarado et al. 2013). However, the number of amphibian species inhabiting dry forests can be astonishingly high, with numerous uniquely adapted species that can withstand the scarcity and uncertainty of water and food during dry seasons (Ceballos 1995a, Chazdon et al. 2011, Stoner and Timm 2011, Ceron et al. 2023). They have evolved adaptations facilitating their survival and persistence in such adverse conditions, limiting their ability to adapt to anthropogenic changes (Székely et al. 2018a, b, Calvo-Alvarado et al. 2013). Therefore, many of these species are threatened because of their narrow ranges and abrupt demographic declines caused by human intervention and habitat destruction and degradation (Newbold 2018, Menéndez-Guerrero et al. 2020).

The NSDFs consist of several natural fragments of variable size, occurring in dispersed subregions, and with different environmental conditions and floristic compositions. They are classified based on plant richness and phylogenetic relatedness, in different regions and subregions taking into consideration the limited dispersal of their most outstanding and dominant plants (Pennington et al. 2009). The resulting biogeographical configuration has been successfully used to explain bird diversity (Prieto-Torres et al. 2019). However, in the case of amphibians, much less information is available at the continental scale (Crawford et al. 2007, Antonelli et al. 2018). Due to their low vagility (Green 2003, Wollenberg et al. 2011), we expect that biogeographic breaks such as mountain ranges, wide rivers, or oceans should constitute physical barriers to their dispersal (Santos et al. 2009, Simões et al. 2014, Thome et al. 2021). Species-rich ecosystems, such as neighboring rainforests, should be less penetrable due to niche filling and competitive exclusion (Kennedy et al. 2002, Price et al. 2014). As a result, geographic isolation should determine a decrease in similarity between the amphibian communities of NSDF subregions (Antonelli et al. 2018). This should also be associated with a higher proportion of amphibian species which are restricted to more isolated subregion (unique species). These exclusive taxa, with their small ranges and limited dispersal capabilities, probably are highly vulnerable to any disturbance (Becker & Loyola 2008, Whitfield et al. 2016), and, consequently, areas that house such species should constitute conservation priorities. Additionally, regional factors such as the climate stability and the connectivity of the forests remnants must affect the amphibian distribution because they affect the rate of speciation and influence the available species pool (Smith et al. 2005, Buckley & Jetz 2007, Fritz & Rahbek 2012). On the other hand, subregions with larger extensions are expected to have richer assemblages overall, as well as more unique species (Losos & Schluter 2000, Roos et al. 2004).

If at a regional scale, the geographical and historical conditions play an important role in species ranges, at a local scale, environmental factors mostly drive species distribution, especially in the case of ectotherms (Schneider et al. 1998). In this sense, climate conditions such as the mean values of temperature and precipitation and their variation, along with elevation, are recognized among the main factors of global amphibian distribution (Rodriguez et al. 2005, Wiens 2007, Rivas et al. 2021).

Understanding the patterns of amphibian diversity in the NSDF and their ecological determinants is essential for effective conservation actions and management to minimize the impacts of habitat destruction and global warming (Lips et al. 2005). Therefore, it is important to know the distribution patterns across all amphibians inhabiting the NSDFs. Our study aims to synthetize the available records for the amphibian biota across the NSDFs. Further, based on this updated list, we focused on answering the following broad-scale questions: (i) what are the characteristics of the NSDF subregions according to their amphibian species richness, the level of endemism and species turnover between NSDFs areas; (ii) are climate factors (for instance, mean annual temperature and rainfall) related to amphibian richness across the NSDFs; (iii) do spatial characteristics of the subregions (size, connectivity to other NSDF subregions) influence amphibian richness, (iv) are more isolated subregions more likely to harbor a higher proportion of endemic species?

Materials and methods

Study area

We have surveyed all the Neotropical Seasonally Dry Forests (NSDFs) following the biogeographical sectorization proposed by Pennington et al. (2000) (see also Calvo-Alvarado et al. (2013) and Banda et al. 2016). For the cartographic delimitation we used the shapes available in The Nature Conservancy (TNC) (http://maps.tnc.org/gis_data.html), considering all dry forest and shrublands in the Neotropics. These forests are situated in the Americas between the Tropic of Cancer (23.5°N) and the Tropic of Capricorn (23.5°S) (Wright et al. 2009). Finally, the study area consists of nine regions (Antilles, Bolivian and Peruvian Interandean valleys, Bolivian Chiquitano region, Caatinga – Cerrado, Caribbean coast of Colombia and Venezuela, Colombian Interandean valleys, Dry Chaco, Mexico and Central America, and the Pacific coastal Ecuador and Peru), each composed of several subregions, for a total of 42 subregions (see Fig. 1 and Appendix 1). We excluded from analysis two subregions (Lesser Antillean Dry Forests and Patía Valley Dry Forests) for which no amphibian occurrence records were available.

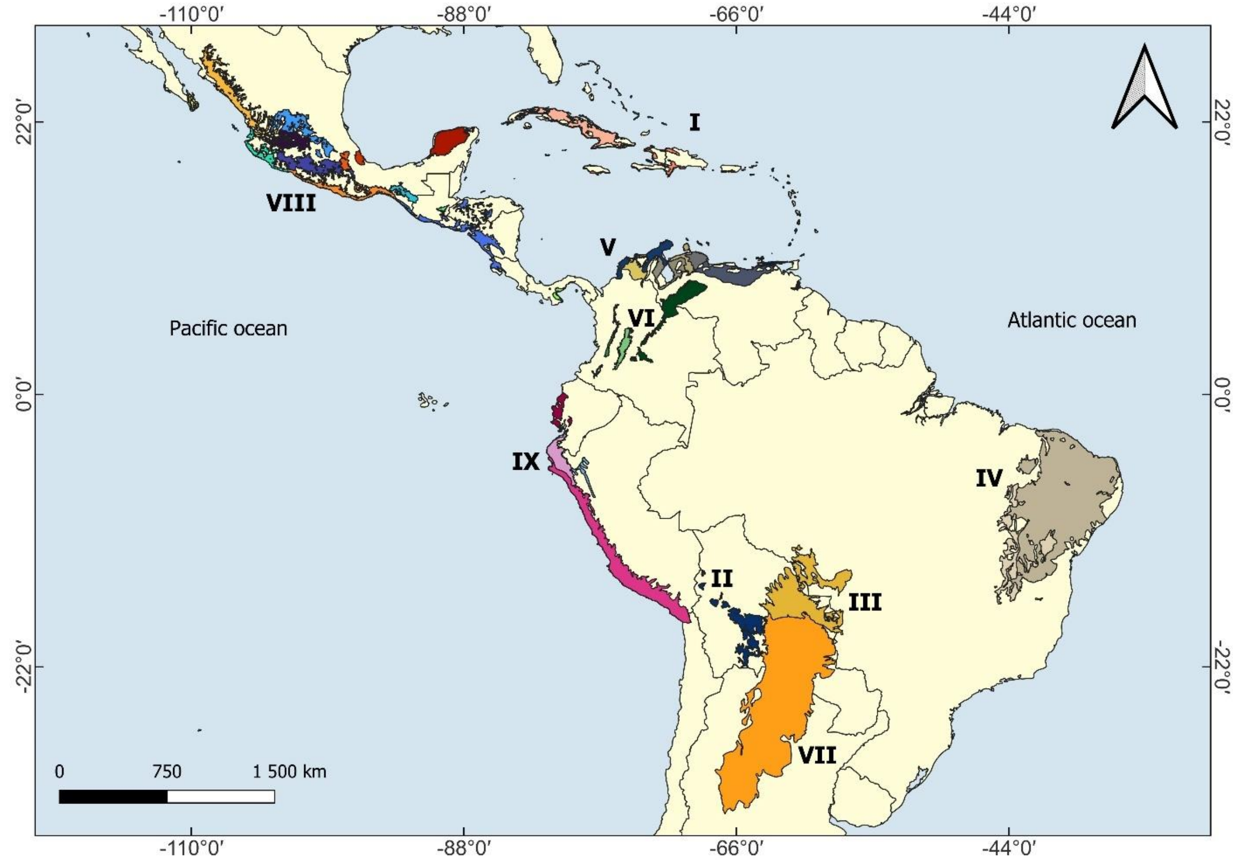

Figure 1. Distribution of the Neotropical Seasonally Dry Forests. These are divided among nine regions: I Antilles, II Bolivian and Peruvian Interandean valleys, III Bolivian Chiquitano region, IV Caatinga – Cerrado, V Caribbean coast of Colombia and Venezuala, VI Colombian Interandean valleys, VII Dry Chaco, VIII Mexico and Central America, IX Pacific coastal Ecuador and Peru. Different colors represent the distinct component subregions.

Data records

We compiled distributional data from museum collections, published articles, online databases and our field generated data. The dataset included only records which were identified to the species level (we eliminated records of species complexes, *incertae sedis*, *affinis* etc.). Taxonomy follows Frost (2023), and the conservation status of each species was assigned following the IUCN (2023) Red List. Doubtful identifications and records which could not be assigned to a currently recognized species, as well as introduced species, were excluded. Duplicated locality records were removed.

The faunal information was collected at the subregion level by overlaying the record of species collections and the cartographic information of the subregions. According to the presence in various subregions, a species is considered unique to the subregion (if it occurs only in one subregion) or shared (if it is present in more than one subregion). We calculated the percentage of uniqueness as the number of unique species/ total number of species in the subregion x 100.

Environmental factors

Environmental and geographical information used to assess the amphibian richness patterns of NSDFs were obtained in Quantum GIS environment 3.4.13 (QGIS.org 2024). For each of the 40 subregions, we estimated the extension (area). As a measure of spatial isolation from other NSDF subregions, we calculated the geographical distance as the smallest distance between the borders for each of the subregions; to obtain the vicinity index, we averaged the distance to the closest five neighbor subregions. As climate factors, we considered annual precipitation, maximum temperature of the warmest month and aridity (Rodriguez et al. 2005, Wiens 2007, Rivas et al. 2021). Climatic historical information regarding precipitation and temperature were downloaded from WorldClim (https://www.worldclim.org/data/index.html; Fick & Hijmans, 2017), with a resolution of 30x30 arcsec (aprox. 1 km^2), while aridity index was obtained from CGIAR Consortium for Spatial Information (https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/), with the same resolution. Using the continental digital elevation model with a 1 km^2 resolution, we obtained the information regarding elevation. For each subregion, we computed the values for these parameters by averaging data from each cell in the subregion. Because higher heterogeneity increases the available ecological niches (Jetz & Rahbek 2002), we also computed the ranges (i.e. difference between the maximum and minimum grid cell value registered in the subregion) for elevation, annual mean temperature, annual precipitation and aridity.

Statistical analysis

To describe the species turnover across subregions, we computed the Sørensen dissimilarity index (β_{Sor}) which can be also dissected in a Simpson dissimilarity (β_{Sim} – the turnover component of Sørensen dissimilarity) and the so-called nestedness dissimilarity (β_{Sne} – the nestedness component of Sørensen dissimilarity) using package "betapart" (Baselga & Orme 2012). We generated a dendrogram relating the various subregions, based on a matrix of species-subregion β_{Sim} pairwise comparisons, since this index is less affected by differences in species richness between samples

(Koleff et al. 2003). We further used a Mantel test to evaluate the correlation between dissimilarity and geographical distances between the subregions, with 10,000 permutations.

To unveil the environmental factors that might influence the overall amphibian richness in each of the subregions, we generated GLMs (assuming a Poisson error distribution and a log link), using as predictors the mean and range values for climate variables (maximum temperature, precipitation, aridity), and geographic factors (extension, elevation). To see the influence of connectivity, we fitted GLMs (Poisson errors, log link) to evaluate if the number of unique species were determined by the subregion extension and the vicinity index. To avoid multicollinearity, before including these in the models, correlation between the various predictors were tested using Pearson correlations. When factors were highly correlated ($r > 0.8$), only the one with a stronger contribution (AIC, r^2) to the model was retained. All factors were standardized for analysis; for extension, we used the area in km^2 (log10 transformed).

All statistical analyses were carried out in R 4.2.0 (R Core Team 2023), with a significance level of $\alpha = 0.05$.

Results

Amphibian diversity in the NSDF

Our final dataset consisted of 43,126 amphibian occurrence records in the NSDFs. These were represented by 260 species, distributed unevenly between 16 families and 56 genera. The richest family was Hylidae (tree frogs), represented by 71 species, followed by Leptodactylidae (51) and Bufonidae (38), which consist of terrestrial/ fossorial species (Fig. 2). Best represented genera are the Leptodactylus (25), Scinax (19), and Eleutherodactylus (19).

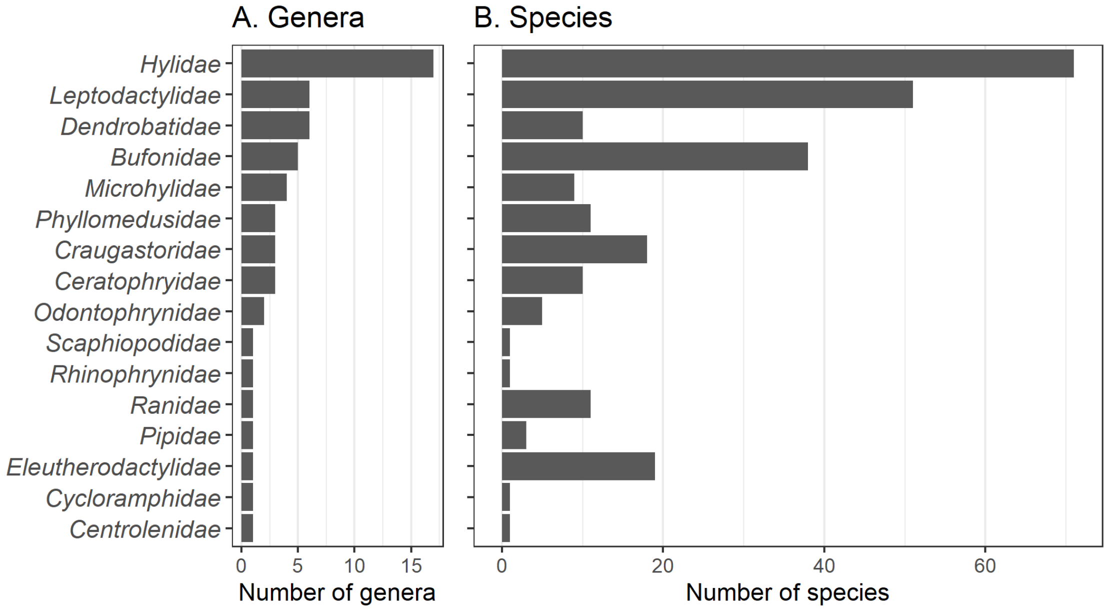

Figure 2. Diversity of the amphibian families from the Neotropical Seasonally Dry Forests, by genera and species.

Out of the 260 amphibian species, 110 were unique at the subregion level, and only 18 species having records from 10 or more subregions. The most widely distributed was *Rhinella marina*, which occurs in 29 of the 40 subregions.

Regarding conservation status, the majority of the amphibians were evaluated as “Least Concern” (90%), the others being “Near Threatened” (3.1%), “Vulnerable” (3.8%), “Endangered” (1.5%) and “Critically Endangered” (1.2%).

Richness by region

The NSDF regions with the highest amphibian richness are Mexico and Central America, Dry Chaco and Caatinga – Cerrado, while the lowest values were found for the Bolivian and Peruvian Interandean valleys. At the genus level, the highest diversity was encountered in the NSDFs of the Caribbean coast of Colombia and Venezuela, Colombian Interandean valleys, and Mexico and Central America (Fig. 3).

The highest percentage of unique species was found in the Pacific coastal Ecuador and Peru (82%) and in the Mexico and Central America region (80%), and also the Antilles (76%) and the Dry Chaco (53%) had a large proportion of their amphibians not shared with other regions (Fig. 3).

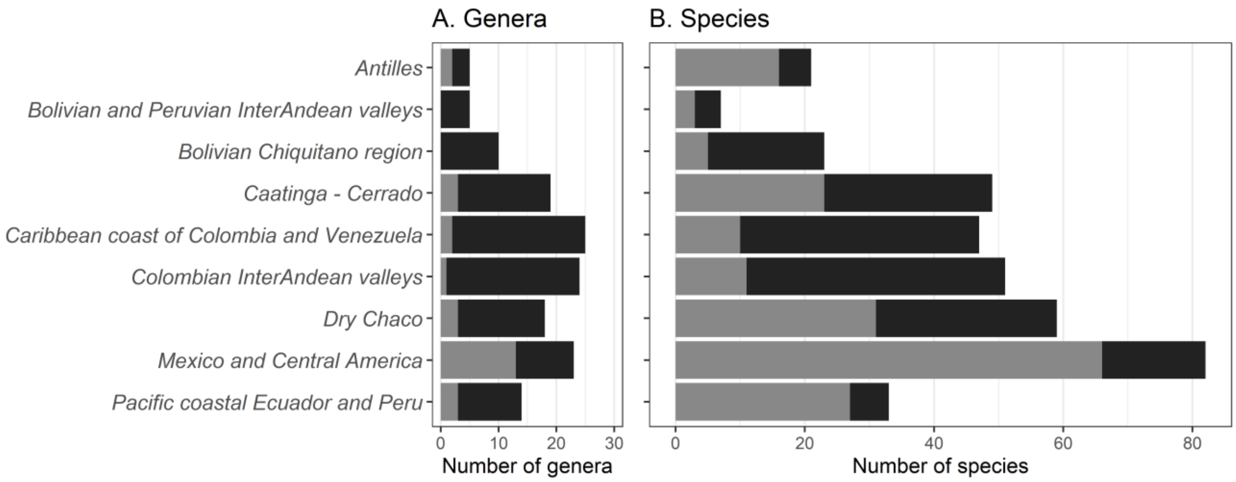

Figure 3. Richness of amphibians in the Neotropical Seasonally Dry Forest regions. In black – number of species shared with at least one other region, in grey – number of species which are unique to the region.

Richness by subregion

At the subregion scale, the highest diversity was encountered in the Dry Chaco and the Caatinga, both with more than a half of the species being unique. Of the 40 subregions, 67.5% housed its set of unique amphibian species. Large proportions of unique amphibians were reported from the Hispaniolan Dry Forests, the Sechura Desert, the Dry Chaco and the Marañon Dry Forests (all over 50%; see Fig. 4).

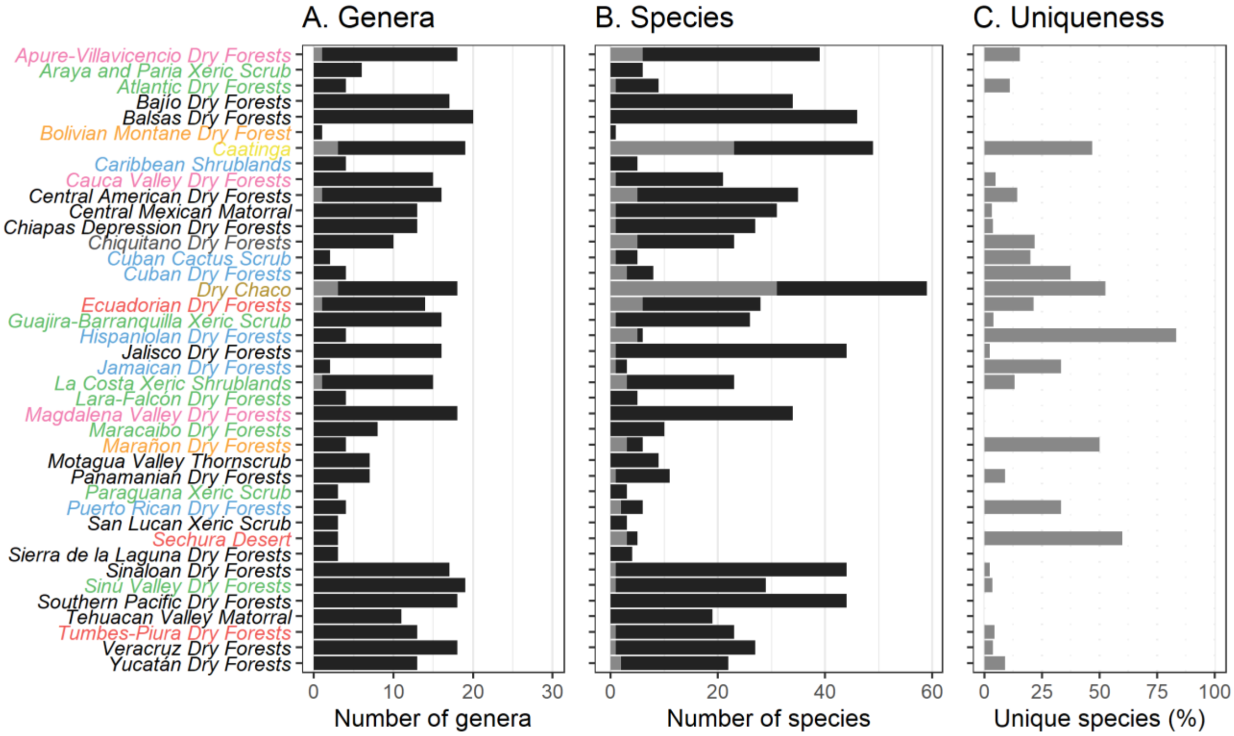

Figure 4. Richness of amphibians by Neotropical Seasonally Dry Forest subregions. In black, number of taxa shared with at least one other region, in grey number of species which are unique to the subregion. Subregions are colored based on the region they belong to: in black - Mexico and Central America, green - Caribbean coast of Colombia and Venezuela, pink - Colombian Inter-Andean valleys, blue – Antilles, yellow - Caatinga – Cerrado, grey - Bolivian Chiquitano region, orange - Bolivian and Peruvian InterAndean valleys, brown - Dry Chaco, and red - Pacific coastal Ecuador and Peru.

The total multi-site dissimilarity across NSDF subregions was $\beta_{\mathrm{Sor}} = 0.96$, with a turnover of $\beta_{\mathrm{Sim}} = 0.92$ and a nestedness of $\beta_{\mathrm{Sne}} = 0.04$. We found that subregions which were geographically closer were more similar in species composition (Mantel test $r = 0.547$, $p < 0.001$), and that they generally followed the same pattern as the vegetation classification, with a few exceptions (Fig. 5).

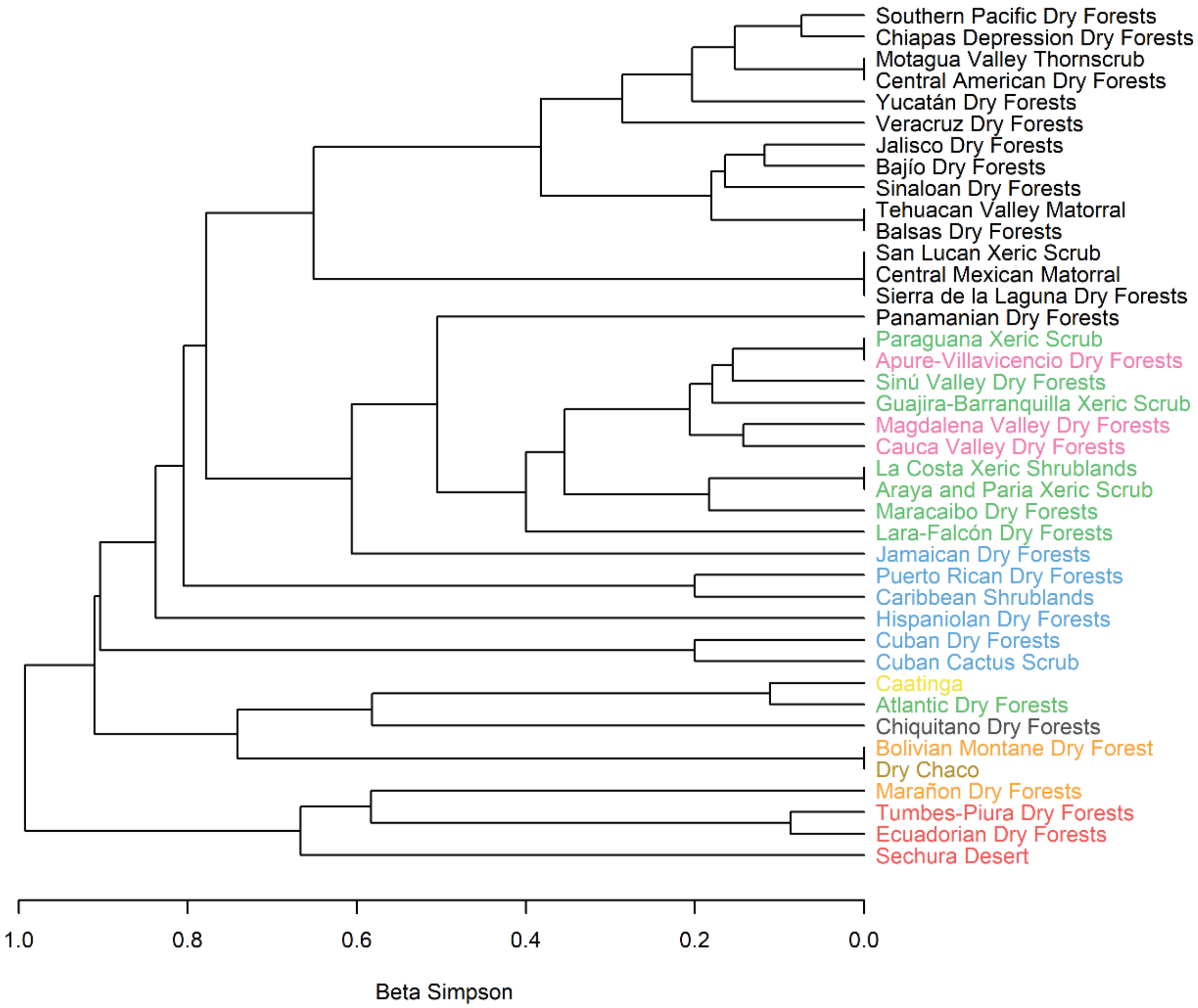

Figure 5. Dendrogram generated from hierarchical clustering of the Neotropical Seasonally Dry Forest subregions based on Simpson dissimilarity index. The X axis shows the distance between clusters. Subregions are colored depending on the region they belong to: in black - Mexico and Central America, green - Caribbean coast of Colombia and Venezuela, pink - Colombian InterAndean valleys, blue – Antilles, yellow - Caatinga – Cerrado, grey - Bolivian Chiquitano region, orange - Bolivian and Peruvian InterAndean valleys, brown - Dry Chaco, and red - Pacific coastal Ecuador and Peru.

Environmental drivers of amphibian richness in the NSDF

The model evaluating richness in each subregion showed that both climate and geographic factors had an important impact (Table 1, Fig. 6). Subregions with larger sizes and more variability in terms of temperature and precipitation registered a higher number of amphibian species. Additionally, the average maximum temperature and the average annual precipitation also had a positive effect on richness. Both area and closeness to neighboring subregions were positively related to the number of amphibians (Table 2).

Table 1. Results of model evaluating the effect of average values of bioclimatic factors on subregion species richness.

Variables	**Estimate**	**Std. Error**	***z***	***p***
Total species richness				
Intercept	-5.5165	0.5992	-9.207	< 0.001
Area	3.3042	0.3924	8.421	**< 0.001**
Elevation range	0.2129	0.2932	0.726	0.47
Temperature range	2.9613	0.3120	9.490	**< 0.001**
Maximum temperature	3.2546	0.5918	5.500	**< 0.001**
Precipitation range	0.8038	0.2268	3.544	**< 0.001**
Average precipitation	0.9353	0.2727	3.430	**< 0.001**

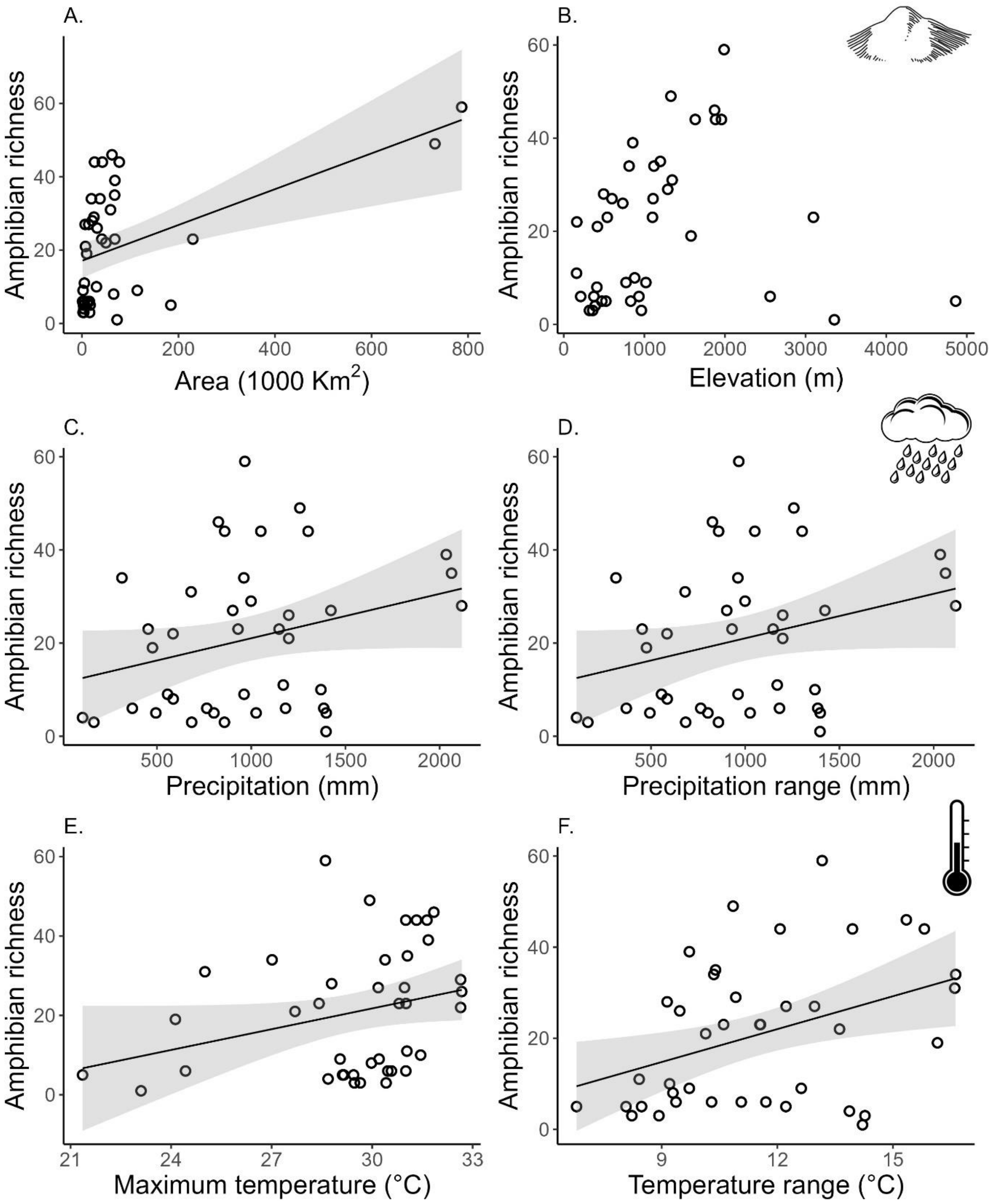

Figure 6. Factors affecting amphibian species richness in the Neotropical Seasonally Dry Forest subregions (n = 40).

Larger subregions also had more unique amphibians (as absolute numbers), regardless of their closeness to other NSDF subregions (Table 2). However, when looking at the percentage of unique species out of the total subregion richness, neither extension nor distance to its neighbors played an important role.

Table 2. Results of the model evaluating the effect of area and closeness to the nearest five neighbors on the number of amphibian species which are unique to each of the subregions.

Variables	**Estimate**	**Std. Error**	***z***	***p***
Total richness				
Intercept	-0.8128	0.2958	-2.748	0.006
Area	5.2520	0.3899	13.469	**<0.001**
Vicinity	-74.0371	12.3566	-5.992	**<0.001**
Unique species richness				
Intercept	-7.1229	0.9945	-7.162	<0.001
Area	9.9.85	1.2387	7.999	**<0.001**
Vicinity	29.7892	25.7459	1.157	0.25
Percentage unique species				
Intercept	106.66	22.67	4.704	<0.001
Area	-21.86	31.16	-0.702	0.49
Vicinity	-2074.23	1096.31	-1.892	0.07

Discussion

We provide the first estimation of the amphibian diversity across the whole Neotropical Seasonally Dry Forests. Evidently, the amphibian fauna in the NSDFs is lower compared to humid biomes, such as the rainforest (Duellman 1988, Fritz & Rahbek 2012, Espinosa et al. 2012). However, despite the strong ecological limitations imposed by the extreme seasonal hydric stress, we found that at least 260 amphibian species are present here. This richness is structured among the various regions and subregions, each showing its unique amphibian assemblages, and highlighting their independent evolutionary history despite having similar environmental pressures. This emphasizes the need to preserve the last remnants of this endangered ecosystem, in order to protect this highly threatened group of vertebrates, similarly to other elements of their biodiversity (Ceballos & Garcia 1995, Portillo-Quintero et al. 2015, Banda et al. 2016).

The Dry Chaco, the Caatinga and the Mexican and Central American regions are widely recognized for their richness and distinctiveness in many taxa (e.g., woody plants, birds, mammals – Ceballos 1995b, Linares-Palomino et al. 2011, Prieto et al. 2019). Our results show that this is also the case for amphibians. This can be explained by the fact that they are surrounded by other species rich ecosystems favoring opportunities for colonization, compared to disconnected regions such as the Caribbean islands or the dry valleys of Peru, which are border by oceans, deserts or high mountain ranges acting as strong dispersal barriers in the case of amphibians (Crawford et al. 2007). Additionally, their sheer size offers a higher diversity of niches. However, some of the smallest NSDF regions also showed surprisingly high levels of species endemism or diversity, such as the Pacific coastal Ecuador and Peru or the Antilles.

Both climate and history affected species ranges, as well as the composition of the corresponding assemblages (Schneider et al. 1998). We found that both water availability (precipitation), energy availability (temperature), as well as their seasonal heterogeneity, were significant predictors of amphibian richness for the NSDF subregions. This is to be expected for these cold-blooded and water-dependent tetrapods (Duellman & Trueb 1994, Ficetola & Maiorano 2016). These factors have been shown to be important both at global and local scales (Buckley & Jetz 2007, Wiens 2007, Paúl et al. 2023). On the other hand, altitude did not play an important role in our model. In parallel, and as predicted by the island biogeography theory (MacArthur & Wilson 2001), we found a positive relationship between the subregion size and the number of species. This can be explained by the higher environmental heterogeny (i.e., available niches) that generally occurs over larger extensions, as well as more potential for colonization from neighboring ecosystems.

As expected, compared to more mobile taxa, such as birds, the degree of overlap in species between various subregions is lower in amphibians. We attribute this to the fact that the contrasting neighboring biomes share relatively little in terms of phylogenetic lineages (e.g. Särkinen et al. 2011), limiting the biotic interchange between different NSDF regions. This is also supported by the fact that community similarity was explained by spatial distance.

The grouping of subregions inside the regions mostly followed the one based on floristic composition (Pennington et al. 2009), with a few remarkable exceptions. The amphibian assemblages from the Panamanian Dry Forests were more related with the Caribbean coast of Colombia and Venezuela and the Colombian Inter-Andean valleys than with the Mexico and Central America region, while the communities in the Marañon Dry Forests were nested inside the Pacific coastal Ecuador and Peru clades. This emphasizes the differences in dispersal patterns and phylogenetic histories between taxa.

Worth to note that dry biomes have a lower sampling effort than their rainforest counterpart, especially in the Neotropics (Ramos et al. 2020, Silva et al. 2020). Poor sampling of vast areas affects biodiversity estimates, especially if this occurs in regions with high endemism levels. Vast NSDF areas have never been adequately surveyed (Garda et al. 2017, Armijos-Ojeda et al. 2021). Sampling for amphibians in the dry forests has an additional complication – the brief reproductive and activity season can be highly unpredictable, so that visits made outside this ideal time frame can be unrepresentative for detecting the presence of many species (Székely et al. 2018a). There is an urgent need for targeted research and detailed inventory efforts for the long-term protection of these species.

This diminished research effort is also suggested by the recent description of several species which are endemic to the NSDFs (Ron et al. 2010, 2018, Menéndez-Guerrero et al. 2024), which is surprising considering that the dry forests are heavily inhabited by human communities (Djoudi et al. 2015). Taxonomy lags affect our understanding of distributional patterns (Simões et al. 2014, Moraes et al. 2016), and these areas have been shown to have a potential to house still many undescribed species (Joppa et al. 2011). The lack of information is likely to be reflected in an exclusion of these habitats from the protected area network, leaving their biodiversity vulnerable to increased human driven pressure.

The vast majority (90%) of the amphibian species inhabiting the NSDFs are considered "Least Concern", and around 7% are assessed as threatened. When tacking into consideration the enormous pressures to which the NSDFs are exposed, mainly related to deforestation and declining habitat, this is surprising and seems to suggest that the evaluations might be outdated. Less than 11% of the NSDFs extension is currently included in protected areas (Prieto-Torres et al. 2019), indicating that protection levels will probably prove to be inadequate in the future. Even when the protected area limits fit well the current range of the species, climate change might lead to inadequate protection in the future, due to modification in the environmental conditions, resulting in projected changes in distribution and local extinctions (Medina et al. 2020, Ballesteros-Barrera et al. 2022). This emphasizes the need for designing flexible and integrative protected areas, which take into account the effects of global changes and rely on landscape connectivity (Prieto-Torres et al. 2016, 2021).

We found that small subregions harbor unique fauna, and it is likely that the effects of global climate change are more detrimental in such isolated, small, fragmented, and highly threatened sites (Portillo-Quintero & Sánchez-Azofeifa 2010, Tapia-Armijos et al. 2015). To make matters worse, the representativeness of protected areas in these regions is also very low (Prieto-Torres et al. 2021). The high species turnover between the NSDF regions, coupled with particularities in geology, geography (dispersal barriers) and human-impact, emphasizes the fact that global change might have distinct impacts on different subregions.

Understanding the large-scale patterns of biodiversity distribution is critical for conservation. The information provided here can be used by decision makers to develop protection and restoration strategies that contribute to amphibian conservation in Neotropical dry ecosystems. Recent studies predicting the effects of the global climate change on the biota of dry biomes give contradicting evidence, going from positive to negative, although when including the effects of other disturbance factors along with that of climate the results suggest a general loss of biodiversity resilience (Manchego et al. 2017, Reyer et al. 2017). There is an urgent need to increase research efforts that allow us to understand the dynamics of NDSFs and can support conservation measures, especially in the context of global climate change, which is predicted to have a disproportionate effect on these habitats (Aide et al. 2013, Siyum 2020).

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Appendix 1. Regions and subregions of the Neotropical Seasonally Dry Forests, their area (in 1,000 km^2, the total number of amphibian species, as well as what percentage of them are unique (i.e., found in no other subregion) and what percentage of them are threatened (i.e., assigned Vulnerable, Endangered, or Critically Endangered, according to the IUCN Red List).

Region	**Subregions**	**Area**	**Total species**	**Percentage unique**	**Percentage threatened**
Antilles	Caribbean Shrublands	3.12	5	0	0
Antilles	Cuban Cactus Scrub	3.26	5	20	20
Antilles	Cuban Dry Forests	65.75	8	37.5	0
Antilles	Hispaniolan Dry Forests	15.45	6	83.3	16.7
Antilles	Jamaican Dry Forests	2.31	3	33.3	0
Antilles	Puerto Rican Dry Forests	1.27	6	33.3	33.3
Bolivian and Peruvian InterAndean valleys	Bolivian Montane Dry Forest	72.78	1	0	0
Bolivian and Peruvian InterAndean valleys	Marañon Dry Forests	11.32	6	50	16.7
Bolivian Chiquitano region	Chiquitano Dry Forests	229.78	23	21.7	0
Caatinga - Cerrado	Caatinga	731.37	49	46.9	0
Caribbean coast of Colombia and Venezuela	Araya and Paria Xeric Scrub	5.26	6	0	0
Caribbean coast of Colombia and Venezuela	Atlantic Dry Forests	114.67	9	11.1	0
Caribbean coast of Colombia and Venezuela	Guajira-Barranquilla Xeric Scrub	31.49	26	3.8	0
Caribbean coast of Colombia and Venezuela	La Costa Xeric Shrublands	68.19	23	13	0
Caribbean coast of Colombia and Venezuela	Lara-Falcón Dry Forests	16.87	5	0	0
Caribbean coast of Colombia and Venezuela	Maracaibo Dry Forests	30.09	10	0	0
Caribbean coast of Colombia and Venezuela	Paraguana Xeric Scrub	15.91	3	0	0
Caribbean coast of Colombia and Venezuela	Sinú Valley Dry Forests	24.88	29	3.4	0
Colombian InterAndean valleys	Apure-Villavicencio Dry Forests	68.25	39	76.2	0

Colombian InterAndean valleys	Cauca Valley Dry Forests	7.31	21	3.4	0
Colombian InterAndean valleys	Magdalena Valley Dry Forests	19.55	34	0	0
Dry Chaco	Dry Chaco	786.82	59	52.5	0
Mexico and Central America	Bajío Dry Forests	37.39	34	0	2.9
Mexico and Central America	Balsas Dry Forests	62.25	46	0	6.5
Mexico and Central America	Central American Dry Forests	67.77	35	14.3	2.9
Mexico and Central America	Central Mexican Matorral	59.19	31	3.22	3.2
Mexico and Central America	Chiapas Depression Dry Forests	13.97	27	3.7	3.7
Mexico and Central America	Jalisco Dry Forests	26.05	44	2.3	6.8
Mexico and Central America	Motagua Valley Thornscrub	2.33	9	0	0
Mexico and Central America	Panamanian Dry Forests	5.09	11	9.1	9.1
Mexico and Central America	San Lucan Xeric Scrub	3.87	3	0	0
Mexico and Central America	Sierra De La Laguna Dry Forests	3.98	4	0	0
Mexico and Central America	Sinaloan Dry Forests	77.36	44	2.3	6.8
Mexico and Central America	Southern Pacific Dry Forests	42.28	44	0	2.3
Mexico and Central America	Tehuacan Valley Matorral	9.86	19	0	5.3
Mexico and Central America	Veracruz Dry Forests	6.616	27	3.7	0
Mexico and Central America	Yucatán Dry Forests	49.63	22	9.1	0
Pacific coastal Ecuador and Peru	Ecuadorian Dry Forests	21.19	28	21.4	10.7
Pacific coastal Ecuador and Peru	Sechura Desert	184.23	5	60	20
Pacific coastal Ecuador and Peru	Tumbes-Piura Dry Forests	41.1	23	4.3	8.7

CAPÍTULO II

Amphibians of the Equatorial Seasonally Dry Forest of Ecuador and Peru

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Abstract

Seasonally dry forests (SDFs) are one of the most challenging ecosystems for amphibians, fueling the diversity of this group of vertebrates. An updated inventory of native amphibians present in the Equatorial SDF is provided, which extends along the Pacific coast of Ecuador and northwestern Peru. The study is based on an extensive field sampling (two thirds of the total records) carried out throughout the Equatorial SDF, along with a compilation of the available information on distribution of amphibians in the region from published scientific papers, museum collections and on-line databases. The final dataset included 2,032 occurrence records for 30 amphibian species, belonging to eight anuran families. Additionally, data regarding conservation status, habitat use, spawn deposition site, reproductive mode, and body size, along with an identification key for all encountered species are provided. The results indicate a strong sampling bias with a deficit in the Peruvian part of the study area, and a need for urgent inventories targeted at under-sampled areas, using modern taxonomic methods. The study emphasizes the conservation priorities in the Equatorial SDF, based on the distribution, conservation status and life-history data. This information should be useful for the local authorities and institutions involved in the management and conservation of biodiversity in SDF.

Key words: Annotated list, Anura, Conservation, Distribution, Herpetofauna, Life-history.

Introduction

Seasonally dry forests (hereafter SDFs) have been recently recognized as a coherent biome distributed across South America (Prado and Gibbs 1993; Pennington et al. 2000; Pennington et al. 2006; Linares-Palomino et al. 2011). They consist of tree- or shrub-dominated ecosystems with deciduous or semideciduous vegetation, occurring in frost-free areas with mean annual temperatures higher than 17ºC, high seasonal rainfall that sums less than 1,600 mm/year, and at least 5-6 months annually with less than 100 mm/month (Murphy and Lugo 1986; Pennington et al. 2000; Prado 2000, Espinosa et al. 2012). Although animal diversity of Neotropical SDFs has received relatively little attention (Sánchez-Azofeifa et al. 2005), a general trend of lower species richness is apparent when compared to neighboring moister forest ecosystems such as rainforests and cloud forests (Espinosa et al. 2011; Hanson 2011; Jenkins et al. 2013; Guedes et al. 2018).

This trend is quite evident in amphibians, organisms that are highly dependent of humid conditions. The harsher climate conditions typical for the SDF act as strong limiting factors for amphibian diversity (Duellman 1988; Székely et al. 2016). Even so, survey efforts carried out in these habitats have revealed high levels of amphibian endemism, and diverse behavioral and physiological adaptations allowing most of these species to endure long periods of low food availability and hydric stress (Ceballos 1995; Chazdon et al. 2011; Stoner and Timm 2011).

In the Neotropics, there are at least four distinct phytogeographic groups of SDF: Caribbean-Mesoamerican, Ecuadorian-Peruvian, Brazilian Caatinga, and Central South American (Prado 2000, Linares-Palomino 2004a). Among them, the Ecuadorian-Peruvian SDF has the smallest extent, aggregating coastal SDFs from western Ecuador and northwestern Peru (Pennington et al. 2000; Peralvo et al. 2007), but excluding the seasonal habitats from Huancabamba and Marañon, which, although relatively close spatially, are considered to be biogeographically distinct due to the fact that the Andes mountain-range represents a dispersal barrier (Linares-Palomino 2004b). Chapman (1926) was the first to recognize the high levels of biodiversity and endemism of the Ecuadorian SDF, using the term Tropical Arid Fauna. Later, the name Tumbesian Centre of Endemism has been extensively used (Cracraft 1985; Best & Kessler 1995; Stattersfield et al. 1998) for this biogeographic region, recognized as a center of endemism at a global scale taking into consideration the better studied taxa, i.e., birds (Best and Kessler 1995) and vascular plants (Davis et al. 1997) and, consequently, a global priority for conservation (DryFlor 2016) and a hotspot for biodiversity (Myers et al. 2000). Other authors have referred to this area under different (complete or partially synonym) names: Ecuadorian Subcentre (Müller 1973), Guayas Province (Ringuelet 1975), Ecuadorian Pacific Dry Forest (Udvardy 1975), Pacific Equatorial Dominion (Ab'Saber 1977), Tumbesian Centre (Cracraft 1985), Ecuadorian Dry Forest and Western Ecuador Moist Forest (Dinnerstein 1995), Western Ecuador Province (Morrone 1999), Arid Ecuadorian and Túmbes–Piura Provinces (Morrone 2001), Equatorial Pacific Area (Porzecanski and Cracraft 2005), Western Ecuador and Ecuadorian Provinces (Morrone 2014), and there is currently a lack of consensus about the precise position and extent of the SDF in Ecuador and Peru. These diverse definitions are usually based on endemism patterns of either vascular plants or birds, so they tend to include neighboring moist habitats, ranging from mangroves to montane cloud forests (Best and Kessler 1995), merging different ecosystems which are often not characterized by seasonality. As a result, these delimitations are less effective when applied to more water-dependent taxa such as amphibians, which show quite different patterns of diversity and endemism.

The amphibian diversity in the SDF of the coastal areas of Ecuador and Peru has been scarcely explored, with only a small number of localities being inventoried (Almendáriz and Carr 1992, 2012; Venegas 2005; Cisneros-Heredia 2006; Armijos-Ojeda and Valarezo 2010; Amador and Martinez 2011; Székely et al. 2016; Sánchez-Nivicela et al. 2015; Cuadrado et al. 2020). Several factors influence this lack of information, including bias caused by researchers' preference for the more biodiverse tropical rain and cloud forests, logistic limitations imposed by site accessibility, and the short and unpredictable rainy season when amphibians are active and can be detected.

The first step in the development of any effective management and conservation strategy for amphibians is the completion of regional inventories, especially in the context of rapid biodiversity loss and climate changes. Understanding species distribution is especially urgent in the case of amphibians, the most threatened vertebrate group worldwide (Catenazzi 2015). In this context, our aim was to update the list of amphibian species and their distribution in the coastal SDF of Ecuador and Peru, through extensive fieldwork and the compilation of all available information, to prioritize conservation actions, promote public awareness and focus further inventory efforts towards areas where gaps remain.

Materials and methods

Study area

For the purpose of the study, we use the definition of the Ecuadorian Province (Morrone 2014), including all seasonally dry forests (SDFs) in this biogeographical region and excluding neighboring moist habitats that are likely to promote amphibian communities of different origin and with different characteristics. Henceforth, we will use the term Equatorial SDF for this area, which has a finer resolution than the one of Ecuadorian Province; also, we consider the term to be more adequate to denominate territories in both Ecuador and Peru. To generate the map layer used in the analysis, we used Quantum GIS (QGIS) environment 3.4.13 (QGIS.org 2021). To delimit our study area, we used as a basis the national digital maps of ecosystem types for Ecuador (MAE 2013) and Peru (MINAM 2019). These two cartographic databases are currently the most precise available for the area, due to their spatial resolution (scale 1:100,000). In both cases, the ministries of environment in the respective countries define the types of ecosystems according to vegetation cover, bioclimate, biogeography, physiography, altitude, and land use cover. The final map for the Equatorial SDF included ecosystem types with a characteristic of seasonal distribution of precipitation and a semi-deciduous and deciduous vegetation (forests, shrublands), and excluded the Marañón dry forests (Suppl. Table 1). We added the “Anthropical” and “No data” categories situated in areas of historical distribution of those ecosystems. The resulting shape was manually corrected, fixing geometry problems and filling gaps with the dedicated tool of QGIS to reduce the noise and obtain a more accurate area. The final area covers 55,680.5 km2 (of which 36.5% in Ecuador and 63.5% in Peru), with an altitudinal range between 0 and 1631 m a.s.l., and consists of a narrow band (3–150 km wide) bordering the Pacific Ocean, extending from the Ecuadorian province of Esmeraldas in the north, to the Peruvian department of Lambayeque in the south.

The climate in the Equatorial SDF region is characterized by a striking seasonality, with a dry season lasting between five and eight months (Escribano-Ávila 2016), a fairly stable high temperature throughout the year, and annual rainfall varying between 500-1,500 mm, while the average monthly rainfall varies between 10 mm to more than 200 mm (Murphy and Lugo 1986; Espinosa et al. 2012). The vegetation is dominated (>50%) by deciduous or semi-deciduous trees. The region is delimited by neighboring ecosystems characterized by a higher rainfall input, such as the transition zones to the Andean mountain range (foothills) in the eastern region and transition zones to the Choco rainforest in the north.

Data collection

The distribution records were compiled from the following sources:

1) Field surveys. Field data were collected and geo-referenced by the authors between 2000 and 2021. Sampling was carried out at various locations (Fig. 1 – Field data), using visual / auditory encounter surveys and active searches (Heyer et al. 1994). Specific methodologies varied, but consisted in both diurnal and nocturnal extensive surveys carried out mainly during the rainy season, and included searches of suitable terrestrial refugia, netting, torching, pitfall traps and call surveys, unconstrained by time or area.

2) Literature review. We carried out search routines between January and April 2021 on the online search engines Google Scholar (https://scholar.google.com/), ScieLO (https://scielo.org/), Web of

Science (http://webofknowledge.com/), retrieving papers by using the following search terms: "amphibian", "Anura", "herpetofauna", and "Tumbesian", "Ecuadorian dry forest", "Peruvian dry forest", and reviewing the first 200 results for each search. We included articles in peer-reviewed journals, as well as theses and reports that included relevant information regarding the species distribution, where locations were either geo-referenced or precise enough to permit the assignation of coordinates, and identification was done to species level (Fig. 1 – Literature).

3) Museum biological collections housed at Instituto Nacional de Biodiversidad, Quito, Ecuador (DHMECN), and Museo de Zoología, Universidad San Francisco de Quito, Ecuador (ZSFQ).

4) Publicly available species distribution data on the Global Biodiversity Information Facility (https://www.gbif.org/), which includes the iNaturalist platform data, accessed April 2021 (https://doi.org/10.15468/dl.55dnar). These data were manually curated, removing all vague locality descriptors, likely erroneous species identification, and exotic species records (Zizka et al. 2020). We also filtered for duplicated records (same species at the same coordinates at the same moment).

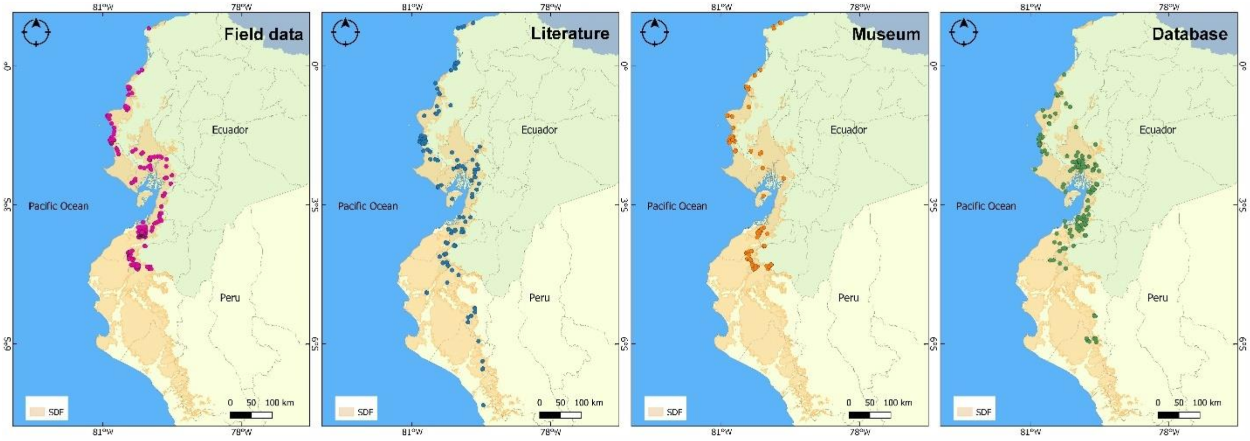

Figure 1. Distribution of amphibian occurrence records in the Equatorial seasonally dry forest (SDF). Maps are provided depending on the data source: Field data, Literature, Museum, Database.

Regardless of source, we standardized the species list using the taxonomy of Amphibian Species of the World (Frost 2021). Only specimens that could be identified to species level were included in the dataset. Non-native species records were removed (i.e., the bullfrog Lithobates catesbeianus). For each species, we indicate the extinction risk status at the global level based on the IUCN Red List of Threatened Species (IUCN 2021), and at the national level based on Ortega et al. (2021).

To characterize species life-history traits, we carried out a literature search for each species in peer-reviewed articles or books and completed with field observations whenever available (Appendix 1). We selected four relevant traits which reflect ecological strategies, niche, and functional roles in the ecosystem (Oliveira et al. 2017) and adopted some rather coarse categories to accommodate for the lack of ecological information for most of the species present in the region. Species habitat use, defined as the overall vertical foraging stratum preferred by the adult, resulted in four broad categories: terrestrial/fossorial (foraging mostly on the ground or in leaf-litter, galleries, crevices, or holes on the floor), arboreal (predominantly perching on leaves in trees, bushes, phytotelmata, grasses, including riparian vegetation), terrestrial/riparian (found in terrestrial habitats close to or around bodies of water), and aquatic/riparian (semi-aquatic species living in streams or ponds). We also reported the reproductive mode (either larval or direct development), as well as the spawn site, the microhabitat where eggs are deposited (either aquatic, terrestrial, or arboreal). As a morphological character, body size was defined as the maximum snout-vent length (SVL) value known for the species, and we report the value separately for females and males. Finally, we generated an identification key, based on morphological characters. However, it is worth mentioning that in some taxa (e.g., the case of Engystomops spp.) the reliable identification usually requires additional information (such as mating calls).

Specimen collection

In the case of voucher specimens, individuals were photographed, after which they were euthanized using 20% benzocaine, fixed in 10% formalin, and stored in 70% ethanol. Tissue samples for genetic analyses were preserved in 96% ethanol. Specimens are deposited at Museo de Zoología, Universidad Técnica Particular de Loja (MUTPL), and Museo de Zoología, Universidad San Francisco de Quito (ZSFQ) Ecuador. Information on these specimens is included as field data since it was generated by the authors during fieldwork.

Research permits were issued by Ministerio del Ambiente del Ecuador. This study was evaluated and approved by the Ethics Committee of Universidad Técnica Particular de Loja (UTPL-CBEA-2016-001).

Results

The final dataset consists of 2,032 distribution records spread throughout the Equatorial SDF region. Seventy-seven records are from Peru, and 1,955 are from Ecuador (Fig. 1). Our field records constitute most of the data points (Fig. 1 – Field data), i.e. 1,374 records (67.6%). The literature revision produced 285 records (14%) from 29 publications (Fig. 1 – Literature), while the museum collections of INABIO and ZSFQ included 87 records (4.3%, Fig. 1 – Museum). The online databases GBIF and iNaturalist contributed 286 data points, representing 14.1% of the dataset (Fig. 1 – Database).

Overall, we report 30 amphibian species for the Equatorial SDF, belonging to 14 genera and eight families (Figs 2–6); all 30 species were present in Ecuador, of which 16 were also encountered in Peru (Suppl. Table 2). The best represented family was Leptodactylidae (genera Engystomops and Leptodactylus) with eight species. Five species (*Ceratophrys stolzmanni*, *Engystomops montubio*, *E. puyango*, *E. randi* and *Lithobates bwana*) are endemic to the Equatorial SDF. Two, *Epipedobates anthonyi* and *Leptodactylus labrosus*, have a distribution mostly restricted to the Equatorial SDF, with few occurrences in adjacent habitats, characterized by higher humidity/altitude. The remaining 23 species have a wider distribution.

Regarding the global extinction risk status (IUCN 2021), one (*C. stolzmanni*) is classified as Vulnerable, and three are Near Threatened (*E. anthonyi*, *Hyalinobatrachium tatayoi*, and *Hyloxalus infraguttatus*). Two are Data Deficient (*Rhinella alata* and *Engystomops guayaco*) and another three (*R. horribilis*, *Scinax tsachila* and *Trachycephalus quadrangulum*) are currently Not Evaluated, while the remaining 21 species have a Least Concern IUCN status (Table 1).

Figure 2. Amphibian species of the Equatorial seasonally dry forest. A. *Rhinella alata* (photo by Silvia Aldás, https://bioweb.bio); B. *Rhinella horribilis*; C. *Hyalinobatrachium tatayoi*; D. *Ceratophrys stolzmanni*; E. *Epipedobates anthonyi*; F. *Epipedobates machalilla*; G. *Hyloxalus elachyhistus*; H. *Hyloxalus infraguttatus*; I. *Boana pellucens*; J. *Boana rosenbergi*; K. *Scinax*

quinquefasciatus; L. *Scinax sugillatus* (photograph by Santiago R. Ron, https://bioweb.bio); M. *Scinax tsachila*; N. *Smilisca phaeota*; O. *Trachycephalus jordani*; P. *Trachycephalus quadrangulum*; Q. *Engystomops guayaco*; R. *Engystomops montubio*; S. *Engystomops pustulatus*; T. *Engystomops puyango*; U. *Engystomops randi*; V. *Leptodactylus labrosus*; W. *Leptodactylus melanonotus*; X. *Leptodactylus ventrimaculatus*; Y. *Barycholos pulcher*; Z. *Pristimantis achatinus*; AA. *Pristimantis lymani*; AB. *Pristimantis subsigillatus*; AC. *Pristimantis walkeri* (photograph by Santiago R. Ron, https://bioweb.bio); AD. Lithobates bwana. Habitat seasonal change (Reserva Ecológica Arenillas): AE. April (rainy season); AF. December (dry season).

Life-history characteristics

In terms of amphibian species habitat use, 17 (56.7%) are terrestrial / fossorial, nine (30%) are arboreal, two are aquatic / riparian (6.7%), and two are terrestrial / riparian (6.7%) (Table 1). Most species have larval development (25 species, 83.3%), and the five species of Strabomantidae have a direct development (16.7%). Amphibians living in Equatorial SDF exhibit several reproductive strategies for egg deposition; the most common behavior was to deposit eggs directly in the water (17 species, 56.6%, amongst which the five Engystomops species which produce foam nests), terrestrial deposition (12 species, 40%), and one species lays egg clutches on leaves overhanging water (*Hyalinobatrachium tatayoi*). The range of body sizes is wide, with maximum adult size varying between 16 mm (*Epipedobates machalilla*) and 130 mm (*Rhinella horribilis*).

Table 1. Life-history characteristics and conservation status for the amphibians of the Equatorial Seasonally Dry Forest. IUCN Status – extinction risk status according to IUCN (2021): NE - Not Evaluated, DD - Data Deficient, LC - Least Concern, NT - Near Threatened, VU - Vulnerable. Reproductive modes: LDv - Larval Development, DDv - Direct Development. * indicates species with a distribution restricted to Equatorial Seasonally Dry Forest. References are given in Appendix 1. FD - unpublished information collected by the authors during fieldwork.

Family	**Specie**	**IUCN Global Status**	**IUCN National Status**	**Habit**	**Spawn site**	**Reproductive Mode**	**Maximum size (males) mm**	**Maximum size (females) mm**	**References**
Bufonidae	*Rhinella alata*	DD	LC	Terrestrial / fossorial	Aquatic	LDv	43.3	56.2	FD; (1)
Bufonidae	*Rhinella horribilis*	NE	LC	Terrestrial / fossorial	Aquatic	LDv	130.0	160.0	FD; (2); (3); (4)
Centrolenidae	*Hyalinobatrachium tatayoi*	NT	LC	Arboreal	Arboreal	LDv	26.8	31.1	FD; (5); (6)
Ceratophryidae	*Ceratophrys stolzmanni**	VU	VU	Terrestrial / fossorial	Aquatic	LDv	70.4	75.9	FD; (7); (8); (9)
Dendrobatidae	*Epipedobates anthonyi*	NT	NT	Terrestrial / fossorial	Terrestrial	LDv	25.0	27.0	FD; (10); (11)
Dendrobatidae	*Epipedobates machalilla*	LC	LC	Terrestrial / fossorial	Terrestrial	LDv	16.0	17.6	FD; (12); (13)
Dendrobatidae	*Hyloxalus elachyhistus*	LC	EN	Aquatic / riparian	Terrestrial	LDv	24.1	24.8	FD; (12); (14)
Dendrobatidae	*Hyloxalus infraguttatus*	NT	VU	Terrestrial / fossorial	Terrestrial	LDv	20.5	23.4	FD; (12); (15); (16)
Hylidae	*Boana pellucens*	LC	LC	Arboreal	Aquatic	LDv	52.9	61.0	(17); (18); (19); (20); (21); (22)
Hylidae	*Boana rosenbergi*	LC	LC	Arboreal	Aquatic	LDv	90.0	93.2	(19); (23); (24); (25)
Hylidae	*Scinax quinquefasciatus*	LC	LC	Arboreal	Aquatic	LDv	38.2	38.9	(26); (27)
Hylidae	*Scinax sugillatus*	LC	NT	Arboreal	Aquatic	LDv	42.0	45.5	(27); (28)
Hylidae	*Scinax tsachila*	NE	LC	Arboreal	Aquatic	LDv	34.2	36.4	FD
Hylidae	*Smilisca phaeota*	LC	LC	Arboreal	Aquatic	LDv	66.0	78.0	(29)
Hylidae	*Trachycephalus jordani*	LC	LC	Arboreal	Aquatic	LDv	95.4	111.3	FD; (28); (30)

Family	**Specie**	**IUCN Global Status**	**IUCN National Status**	**Habit**	**Spawn site**	**Reproductive Mode**	**Maximum size (males) mm**	**Maximum size (females) mm**	**References**
Hylidae	*Trachycephalus quadrangulum*	NE	LC	Arboreal	Aquatic	LDv	76.9	80.8	FD; (28); (31)
Leptodactylidae	*Engystomops guayaco*	DD	VU	Terrestrial / fossorial	Aquatic	LDv	19.38	20.98	FD
Leptodactylidae	*Engystomops montubio**	LC	LC	Terrestrial / fossorial	Aquatic	LDv	22.8	19.71	FD
Leptodactylidae	*Engystomops pustulatus*	LC	LC	Terrestrial / fossorial	Aquatic	LDv	32.3	36.5	FD
Leptodactylidae	*Engystomops puyango**	LC	NT	Terrestrial / fossorial	Aquatic	LDv	30.5	32.6	FD; (13); (32)
Leptodactylidae	*Engystomops randi**	LC	LC	Terrestrial / fossorial	Aquatic	LDv	18.7	19.7	(13); (33)
Leptodactylidae	*Leptodactylus labrosus*	LC	LC	Terrestrial / fossorial	Terrestrial	LDv	67.4	71.2	FD; (34); (35); (36)
Leptodactylidae	*Leptodactylus melanonotus*	LC	LC	Terrestrial / riparian	Terrestrial	LDv	43.4	48.1	(35); (37); (38)
Leptodactylidae	*Leptodactylus ventrimaculatus*	LC	LC	Terrestrial / riparian	Terrestrial	LDv	55.4	59.3	FD
Strabomantidae	*Barycholos pulcher*	LC	LC	Terrestrial / fossorial	Terrestrial	DDv	26.9	30.5	(39); (40)
Strabomantidae	*Pristimantis achatinus*	LC	LC	Terrestrial / fossorial	Terrestrial	DDv	36.2	46.1	(19); (41); (42)
Strabomantidae	*Pristimantis lymani*	LC	LC	Terrestrial / fossorial	Terrestrial	DDv	45.3	72.9	FD; (43); (44)
Strabomantidae	*Pristimantis subsigillatus*	LC	LC	Terrestrial / fossorial	Terrestrial	DDv	28.5	33.4	FD; (45)
Strabomantidae	*Pristimantis walkeri*	LC	LC	Terrestrial / fossorial	Terrestrial	DDv	18.5	25.3	FD
Ranidae	*Lithobates bwana*	LC	NT	Aquatic / riparian	Aquatic	LDv	63	95	FD; (46)

Changes in distribution range

We report here the extension of the distribution ranges of four amphibian species detected during fieldwork.

Ceratophrys stolzmanni (Pacific horned frog). This species is endemic to the lowland Equatorial SDF (Ortega-Andrade et al. 2021), with a distribution extending from its type locality, Tumbes, Peru (Steindachner 1882), in the south, up to La Seca (Manabí, Ecuador), in the north. Distribution follows the Pacific coast, the innermost point being 50 km from the coast (Cuadrado et al. 2020), but all previously recorded locations were at low altitudes (up to 130 m a.s.l.). In the present study, we extend the known distribution of this species by adding several new locations (Fig. 3). Amongst them, the record from Manabí, Ecuador (1.0679° S; 80.8308° W), in the vicinity of the El Aromo oil refinery, at 380 m a.s.l., is the highest altitude reported for the species. We also encountered the Pacific horned frog in Progreso, Reserva Cazaderos (4.0259° S; 80.4497° W, 221 m a.s.l.) and Mangahurco, Área de Conservación Municipal Los Guayacanes (4.1611° S; 80.4388° W, 360 m a.s.l.), these being the first records for the Loja province (Ecuador). They also represent the most continental records for this species, being located at more than 70 km from the Pacific coast. Another important observation is that the locations in Loja province, despite being spatially close to the Tumbes region, are actually separated by the Cerro de Amotape mountain range, which was until now considered a barrier for this typically lowland, burrowing amphibian.

Engystomops puyango (Puyango dwarf frog). This small amphibian was recently described from the Puyango Petrified Forest, in south-western Ecuador (Ron et al. 2014), and was until now known from a small number of localities. We contribute several new reports in the region; its presence in Casacay (3.3383° S; 79.7268° W, 146 m a.s.l.), El Oro province, more than 72 km from the type locality, constitutes the farthest record from the known distribution (Fig. 4).

Engystomops randi (Rand's dwarf frog). Another recently described leptodactylid species, which has a wider distribution, encompassing most of the Equatorial SDF close to the coast (Ron et al. 2014). We report for the first time its presence in Peru, Tumbes Reserve (3.7743° S; 80.2249° W, 53 m a.s.l.) (Fig. 4).

Trachycephalus quadrangulum (Chocoan milk frog). This is a large tree frog, mostly known from the coastal Ecuadorian region (Ron et al. 2016). We contribute a new locality for Loja province in Ecuador, close to Bolaspamba (4.1823° S; 80.3692° W, 416 m a.s.l.) (Fig. 5).

Key to the amphibian species of the Equatorial seasonally dry forests of Ecuador and Peru

1	Digit tips not expanded	**2**
-	Digit tips expanded	**13**
2	Keratinized metatarsal spade present; extremely wide head and mouth	***Ceratophrys stolzmanni***
-	Keratinized metatarsal spade absent	**3**
3	Parotoid glands present	**4**
-	Parotoid glands absent	**10**
4	Cranial crests present; adults medium or large: SVL > 40 mm; flank glands absent	**5**
-	Cranial crests absent; adults small: SVL < 40 mm; flank glands present	**6**
5	Large sized, SVL of adults > 70 mm; parotoid glands large; tarsal fold present	***Rhinella horribilis***
-	Medium sized, SVL of adults < 60 mm; parotoid glands small; tarsal fold absent	***Rhinella alata***
6	SVL of adults > 23 mm; lateral fringes on toes absent	**7**
-	SVL of adults < 23 mm; lateral fringes on toes present	**8**
7	SVL of adults > 25 mm; larger tubercles on the dorsum	***Engystomops pustulatus***
-	SVL of adults > 23 mm; smaller and fewer tubercles on the dorsum	***Engystomops puyango***
8	SVL of adults 15–20 mm; lateral fringes on toes broad; webbing between toes basal	***Engystomops guayaco***
-	Lateral fringes on toes narrow, webbing between toes absent	**9**
9	SVL of adults 17–22 mm; proportionately shorter flank and parotoid glands	***Engystomops montubio***
-	SVL of adults 17–20 mm; proportionately longer flank and parotoid glands	***Engystomops randi***
10	Extensive webbing between the toes; subarticular tubercles low	***Lithobates bwana***
-	Webbing between the toes absent; subarticular tubercles well developed	**11**
11	Males with black horny thumb spines; toes with well-developed lateral fringes	***Leptodactylus melanonotus***
-	Males without thumb spines; toes without developed lateral fringes	**12**
12	Posterior surface of tarsus with many white tubercles; sole of foot with white tubercles	***Leptodactylus ventrimaculatus***
-	Posterior surface of tarsus usually without white tubercles; sole of foot usually lacking white tubercles	***Leptodactylus labrosus***
13	Expanded discs bearing a pair of scute-like fleshy structures on the dorsal surface of digit tips	**14**
-	Expanded discs without dorsal scute-like fleshy structures on tips of digits	**17**
14	Broad, light middorsal stripe present	***Epipedobates anthonyi***
-	Middorsal stripe absent	**15**
15	Venter immaculate (without white spots)	***Epipedobates machalilla***
-	Venter with white spots	**16**
16	Extensive webbing between the toes	***Hyloxalus elachyhistus***
-	Limited webbing between the toes	***Hyloxalus infraguttatus***

17	Venter transparent with the white peritonea and lungs visible, dorsal surfaces green with yellow spots	***Hyalinobatrachium tatayoi***
-	Venter not transparent and internal organs not visible, dorsal surfaces brown, grey or green	**18**
18	Fingers lacking webbing	**19**
-	Webbing present between fingers	**26**
19	Toe III longer than Toe V; digit tips just slightly expanded (swollen); well defined white glands posterior to angle of jaw	***Barycholos pulcher***
-	Toe V longer than Toe III	**20**
20	Toes lacking extensive webbing	**21**
-	Webbing present between toes	**24**
21	Finger I longer than Finger II; dorsolateral folds present	**22**
-	Finger I shorter than Finger II; dorsolateral folds absent	**23**
22	Discs on fingers relatively small; inner surface of tarsus bearing long fold; posterior surfaces of the thighs black with white spots or reticulations; SVL of adults 25–73 mm	***Pristimantis lymani***
-	Discs on fingers broad; inner tarsal tubercle small; posterior surfaces of the thighs brown with small cream flecks; SVL of adults 23–46 mm	***Pristimantis achatinus***
23	Snout bearing papilla at tip; heel with small conical tubercle; SVL of adults 19–33 mm	***Pristimantis subsigillatus***
-	Snout without papilla at tip; heel lacking tubercles; groin black with yellow spots; SVL of adults 13–25 mm	***Pristimantis walkeri***
24	Lower jaw with a row of tubercles; snout long; black and blue mottling in the groin and on the anterior and posterior surfaces of the thighs	***Scinax sugillatus***
-	Lower jaw without a row of tubercles	**25**
25	Shank bones visible through the skin, white to bluish-white; dorsum with scattered to abundant small tubercles	***Scinax quinquefasciatus***
-	Shank bones visible through the skin, green; dorsum without tubercles	***Scinax tsachila***
26	Top of the head co-ossified and rough (integumentary-cranial co-ossified skull); iris golden with irregular black spots; SVL of adults 65–111 mm	***Trachycephalus jordani***
-	Top of the head not co-ossified	**27**
27	Skin on dorsum tuberculate; webbing between the fingers extensive; dorsal coloration usually brown	***Boana rosenbergi***
-	Skin on dorsum smooth; webbing between fingers basal to moderate	**28**
28	Pronounced calcar on the heel; webbing between the fingers moderate; dorsal coloration usually green; iris yellowish	***Boana pellucens***
-	Calcar on heel absent	**29**
29	Webbing between the fingers moderate; iris golden with irregular black spots; thick, glandular skin on the head and back	***Trachycephalus quadrangulum***
-	Webbing between the fingers basal; characteristic dark postorbital mark and white labial stripe	***Smilisca phaeota***

Clave para las especies de anfibios del bosque estacionalmente seco de la región Pacífico Ecuatorial

1	Terminaciones de los dedos no expandidas	**2**
-	Terminación de los dedos expandidas	**13**
2	Presencia de espádices metatarsiales queratinizados; cabeza y boca extremadamente anchas	***Ceratophrys stolzmanni***
-	Espádice metatarsial queratinizado ausente	**3**
3	Presencia de glándulas parotoideas	**4**
-	Glándulas parotoideas ausentes	**10**
4	Presencia de crestas craneales; adultos medianos o grandes: LHC > 40 mm; glándulas del flanco ausentes	**5**
-	Crestas craneales ausentes; adultos pequeños: LHC < 40 mm; glándulas del flanco presentes	**6**
5	Tamaño grande, LHC de adultos > 70 mm; glándulas parotoideas grandes; pliegue tarsal presente	***Rhinella horribilis***
-	Tamaño mediano, LHC de adultos < 60 mm; glándulas parótidas pequeñas; pliegue tarsal ausente	***Rhinella alata***
6	LHC de adultos > 23 mm; flecos laterales en los dedos de los pies ausentes	**7**
-	LHC de adultos < 23 mm; flecos laterales en los dedos de los pies presentes	**8**
7	LHC de adultos > 25 mm; tubérculos más grandes en el dorso	***Engystomops pustulatus***
-	LHC de adultos > 23 mm; menos tubérculos y de tamaño menor en el dorso	***Engystomops puyango***
8	LHC de adultos de 15 a 20 mm; flecos laterales en los dedos de los pies anchas; membrana entre los dedos de los pies basal	***Engystomops guayaco***
-	flecos laterales en los dedos del pie estrechos; membranas entre los dedos del pie ausentes	**9**
9	LHC de adultos de 17 a 22 mm; glándulas parotoideas y del flanco proporcionalmente más pequeñas	***Engystomops montubio***
-	LHC de adultos de 17 a 20 mm; glándulas parotoideas y del flanco proporcionalmente más largas	***Engystomops randi***
10	Extensas membranas entre los dedos de los pies; tubérculos subarticulares bajos	***Lithobates bwana***
-	Membranas entre los dedos de los pies ausentes; tubérculos subarticulares bien desarrollados	**11**
11	Machos con espinas córneas negras en los pulgares; dedos de los pies con flecos laterales bien desarrollados	***Leptodactylus melanonotus***
-	Machos sin espinas pulgares; dedos de los pies sin flecos laterales desarrollados	**12**
12	Superficie posterior del tarso con muchos tubérculos blancos; planta del pie con tubérculos blancos	***Leptodactylus ventrimaculatus***
-	Superficie posterior del tarso generalmente sin tubérculos blancos; planta del pie generalmente sin tubérculos blancos	***Leptodactylus labrosus***
13	Discos expandidos que llevan un par de estructuras carnosas en forma de escudos en la superficie dorsal de las puntas de los dedos	**14**
-	Discos expandidos sin estructuras carnosas en forma de escudos dorsales en las puntas de los dedos	**17**
14	Presencia de una franja media dorsal clara y ancha	***Epipedobates anthonyi***
-	Franja media dorsal ausente	**15**

15	Vientre inmaculado (sin manchas blancas)	***Epipedobates machalilla***
-	Vientre con manchas blancas	**16**
16	Membrana extensa entre los dedos de los pies	***Hyloxalus elachyhistus***
-	Membrana limitada entre los dedos	***Hyloxalus infraguttatus***
17	Vientre transparente con el peritoneo blanco y los pulmones visibles, superficies dorsales verdes con manchas amarillas	***Hyalinobatrachium tatayoi***
-	Vientre no transparente y órganos internos no visibles, superficies dorsales marrón, gris o verde	**18**
18	Dedos de la mano sin membranas interdigitales	**19**
-	Membranas interdigitales presentes entre los dedos de la mano	**26**
19	Dedo III del pie más largo que el Dedo V; puntas de los dedos solo ligeramente expandidas (hinchadas); glándulas blancas bien definidas posteriores al ángulo de la mandíbula	***Barycholos pulcher***
-	Dedo V del pie más largo que el Dedo III	**20**
20	Dedos del pie que carecen de membranas extensas	**21**
-	Membranas interdigitales presentes entre los dedos de los pies	**24**
21	Dedo I del mano más largo que el Dedo II; pliegues dorsolaterales presentes	**22**
-	Dedo I del mano más corto que el Dedo II; pliegues dorsolaterales ausentes	**23**
22	Discos en los dedos relativamente pequeños; superficie interna del tarso con pliegue largo; superficies posteriores de los muslos negras con manchas o reticulaciones blancas; LHC de adultos 25–73 mm	***Pristimantis lymani***
-	Discos en los dedos anchos; tubérculo tarsal interno pequeño; superficies posteriores de los muslos marrones con pequeñas manchas color crema; LHC de adultos 23–46 mm	***Pristimantis achatinus***
23	Hocico con papila en la punta; talón con pequeño tubérculo cónico; LHC de adultos 19–33 mm	***Pristimantis subsigillatus***
-	Hocico sin papila en la punta; talón sin tubérculos; ingle negra con manchas amarillas; LHC de adultos 13–25 mm	***Pristimantis walkeri***
24	Mandíbula inferior con una hilera de tubérculos; hocico largo; moteado negro y azul en la ingle y en las superficies anterior y posterior de los muslos	***Scinax sugillatus***
-	Mandíbula inferior sin una hilera de tubérculos	**25**
25	Huesos de las patas visibles a través de la piel, de color blanco a blanco azulado; dorso con pequeños tubérculos, dispersos a abundantes	***Scinax quinquefasciatus***
-	Huesos de las patas visibles a través de la piel, verdes; dorso sin tubérculos	***Scinax tsachila***
26	Parte superior de la cabeza co-osificada y rugosa (cráneo co-osificado tegumentario-craneal); iris dorado con manchas negras irregulares; LHC de adultos 65–111 mm	***Trachycephalus jordani***
-	Parte superior de la cabeza no co-osificada	**27**
27	Piel en el dorso tuberculada; membrana extensa entre los dedos de la mano; coloración dorsal generalmente marrón	***Boana rosenbergi***
-	Piel lisa en el dorso; membrana entre los dedos basal a moderada	**28**
28	Calcar pronunciado en el talón; membrana entre los dedos de la mano moderada; coloración dorsal generalmente verde; iris amarillento	***Boana pellucens***
-	Calcar en el talón ausente	**29**

29	Membrana entre los dedos de la mano moderada; iris dorado con manchas negras irregulares; piel glandular gruesa en la cabeza y dorso	***Trachycephalus quadrangulum***
-	Membrana entre los dedos de la mano basal; marca postorbital oscura característica y franja labial blanca	***Smilisca phaeota***

Discussion

We provide the first comprehensive amphibian species checklist for the Equatorial SDF, including 30 species. In addition to compiling the available data from published sources, museum collections and online databases, we contribute a large amount of original information generated through extensive field surveys (two thirds of all reported information for the area). Although the records reported here significantly add to our previous understanding of tropical amphibian communities in South American seasonally dry habitats, the dataset probably underestimates the actual amphibian diversity in the area.

Although the Equatorial SDF has been overall understudied, the lack of information is most evident in the Peruvian part of this ecoregion. For a better understanding, further efforts to disseminate currently unpublished amphibian distribution records of Peruvian researchers and taxonomically clarify the identity of amphibians which are currently assigned only at genus level (e.g., Venegas 2005) are necessary. From the total dataset, less than 4% of the records were from Peru, although 63.5% of Equatorial SDF area corresponds to this country. A lower amphibian richness is expected in certain Peruvian regions, such as the area bordering the Sechuran desert, due to the hostile environmental conditions. The bibliographic search and a comparison with similar habitats in Ecuador suggest that the lack of data regarding amphibian diversity in the Peruvian part of the Equatorial SDF is due to sampling bias rather than accurately reflecting the absence of this taxa. Even in Ecuador, where sampling was carried out more homogenously throughout the study area, there is still a shortage of adequate amphibian inventories, especially outside protected areas (Ortega-Andrade et al. 2021). Further efforts to inventory the extensive underexplored areas to correctly evaluate the amphibian community status should constitute a priority (Ortega-Andrade et al. 2021).

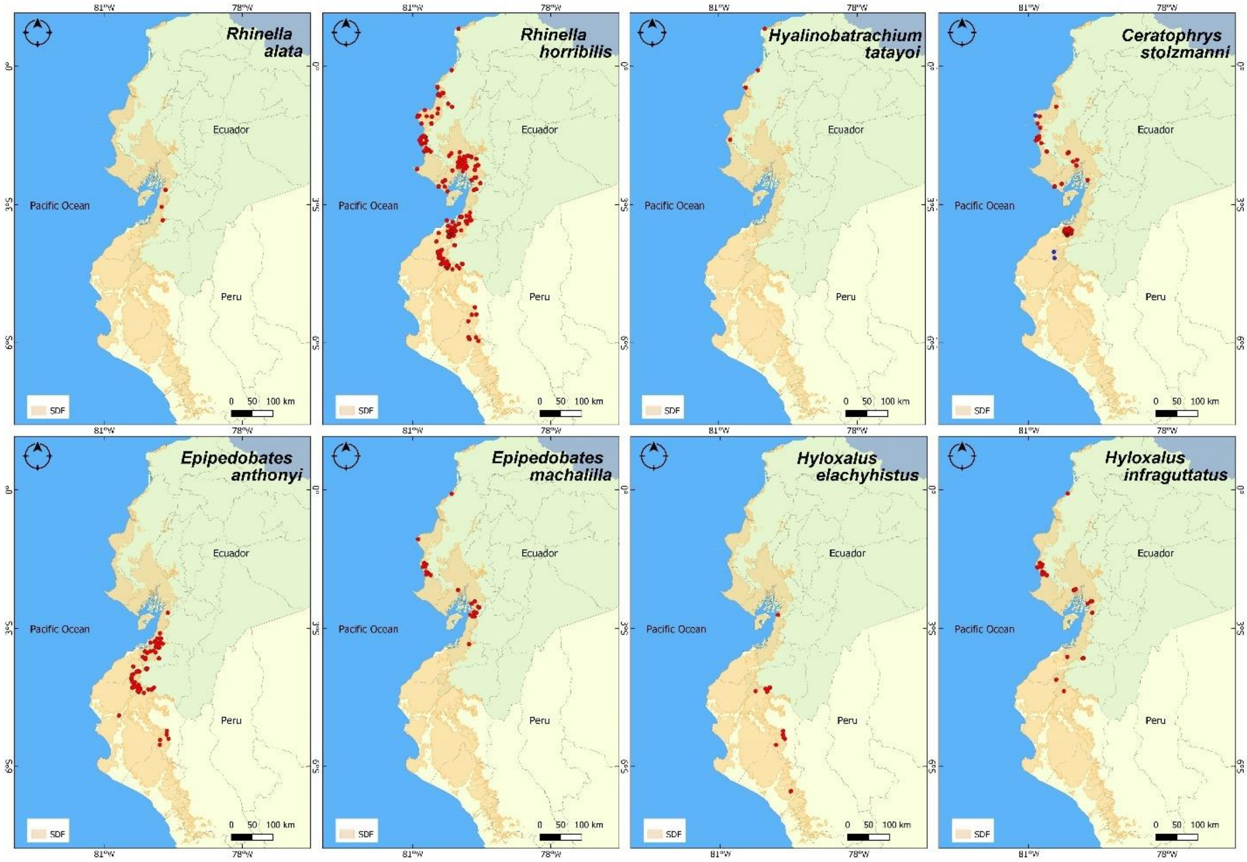

Figure 3. Distribution records of Bufonidae, Centrolenidae, Ceratophryidae and Dendrobatidae in the Equatorial seasonally dry forest (SDF). Maps are given for the families Bufonidae (Rhinella alata, R. horribilis), Centrolenidae (*Hyalinobatrachium tatayoi*), *Ceratophryidae (Ceratophrys stolzmanni*) and Dendrobatidae (*Epipedobates anthonyi*, *E. machalilla*, *Hyloxalus elachyhistus*, *H. infraguttatus*). For *Ceratophrys stolzmanni*, blue points represent new distributional records for the species, the two southernmost localities and the highest altitude, respectively.

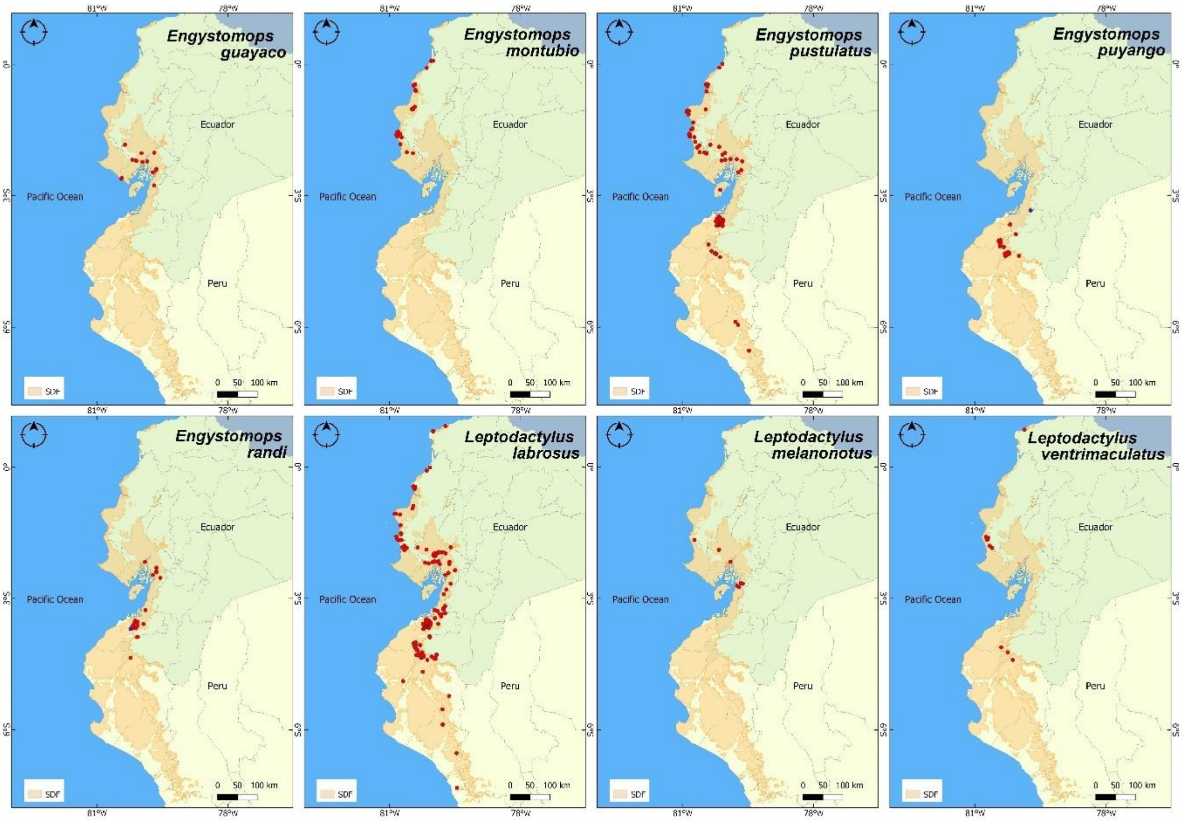

Figure 4. Distribution records for the Leptodactylidae family in the Equatorial seasonally dry forest (SDF). In blue, distribution range extensions: for *Engystomops puyango*, the northernmost locality is more than 70 km from the previously known distribution; for *E. randi*, the first record in Peru.

The fact that, out of the 30 species present in the Equatorial SDF, five have been described as new for science in the last 20 years (Scinax tsachila, Engystomops guayaco, E. montubio, E. puyango, E. randi) further emphasizes the need for intense and focused research targeted at undersampled locations. The list of amphibians present in the Equatorial SDF can change in the future because of updated taxonomic studies based on modern integrative techniques that use morphological, molecular, and behavioral data. It is the case of the cane toads (R. horribilis), for which a recent study indicates that the species present in these forests might be phylogenetically distinct from the rest of the range (Pereyra et al. 2021). Similarly, a species of milk frog (Trachycephalus quadrangulum) was resurrected after being included in the T. typhonius species complex for 50 years, as was the toad Rhinella alata, after being synonymized to R. margaritifera. It is likely that a similar fate awaits species in the genera Pristimantis, Leptodactylus and Hyloxalus, for which taxonomical delimitation is currently based on morphological characters only, allowing for the existence of cryptic taxa.

We include the information on important life history characteristics for all amphibian species present in the Equatorial SDF. It is recommended that prioritization of conservation measures should consider functional diversity of an assemblage, not only species richness, since species make differential contribution to the functioning of their ecosystem (Campos et al. 2017, Bolochio et al. 2020). Currently, research conducted on life-history is scarce for most of the 30 amphibian species. As more information becomes available, the inclusion of additional traits, might offer a more complete image of the native amphibian communities and their capacity to withstand landscape changes. The current insufficient knowledge regarding Equatorial SDF species threats and risks, in addition to the fact that some have been only recently (re)described, results in the five species that are lacking a global conservation status assessment.

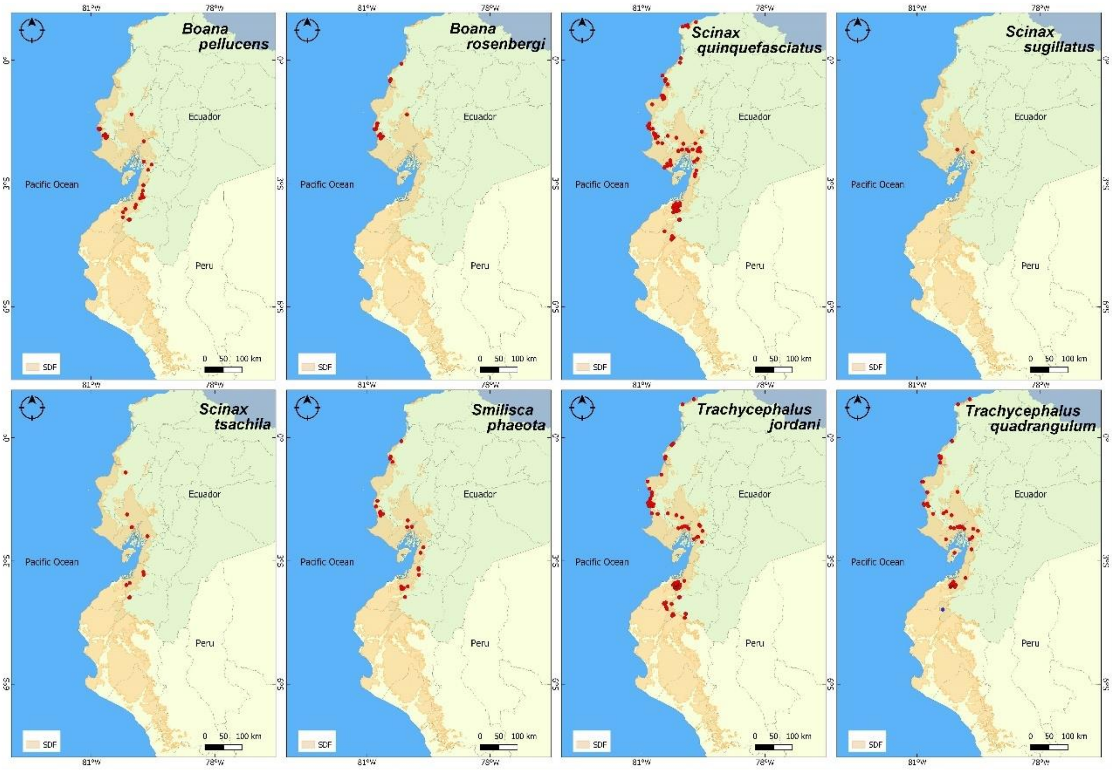

Figure 5. Distribution records for the Hylidae family in the Equatorial seasonally dry forest (SDF). In blue, the first report of *Trachycephalus quadrangulum* in Loja province.

Seven of the 30 species (23.3%) have a distribution exclusively or almost-exclusively restricted to the Equatorial SDF. Although amphibian species living in tropical dry forests are inherently more tolerant to high temperatures and desiccation, they are still expected to be vulnerable to the predicted climate changes because they are already exposed to conditions at the limit of their physiological tolerance (Catenazzi et al. 2014; Székely et al. 2018). No studies modelling the sensitivity to climate change scenarios have been carried out for the species endemic to the Equatorial SDF. Some of the species have adapted to anthropized environments, and in some cases their distribution extends to other ecosystems adjacent to the dry forest. However, the small extent and fragmented limits of the Equatorial SDF, coupled with the land-use change that affects this ecoregion, represent a risk that, in the case of climate change, these species face a reduction of suitable habitat (Nowakowski et al. 2017), even if currently they also occur in protected areas. This emphasizes the need for the species with a narrow distribution to be targeted for urgent monitoring and conservation measures (Sodhi et al. 2008).

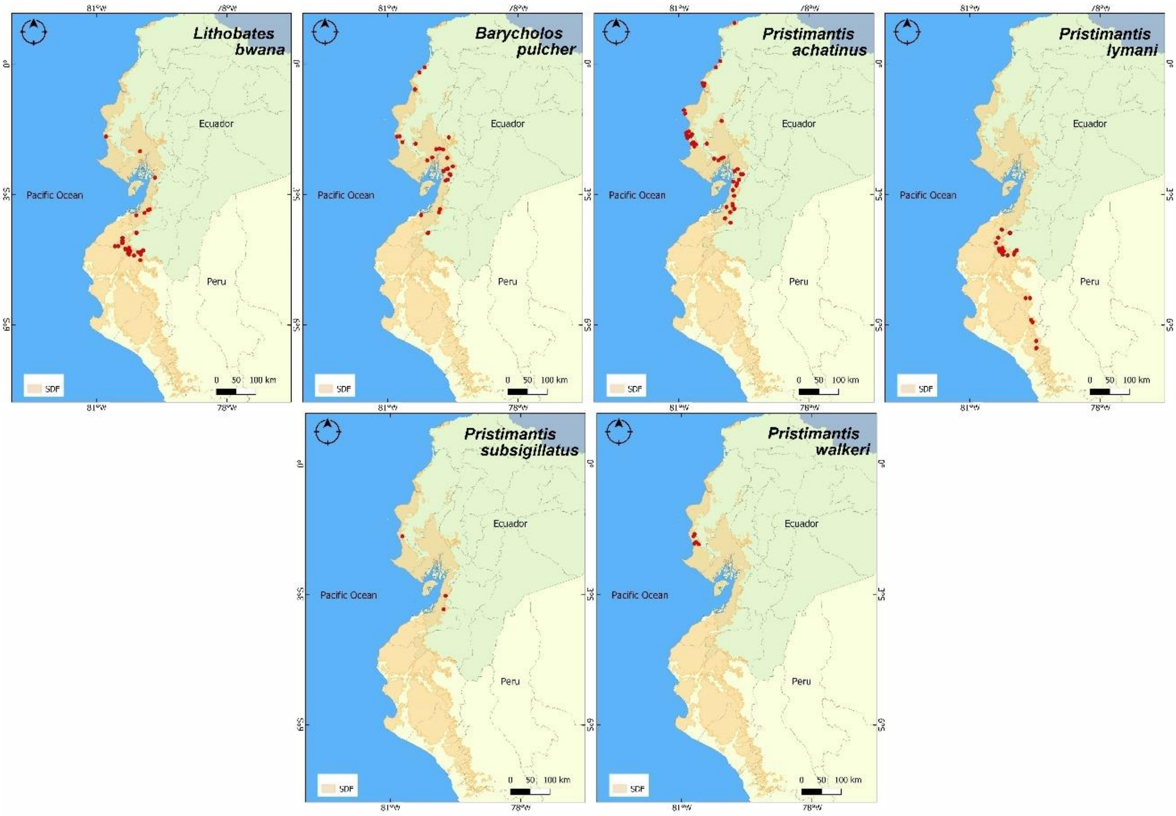

Figure 6. Distribution records of Ranidae and Craugastoridae in the Equatorial seasonally dry forest (SDF). Maps are given for Ranidae (*Lithobates bwana*) and Craugastoridae (*Barycholos pulcher*, *Pristimantis achatinus*, *P. lymani*, *P. subsigillatus*, and *P. walkeri*).

Conservation aspects

The current loss of biodiversity in the study area is the synergic result of a multitude of factors, the most important being habitat loss, fragmentation, pollution, introduction of alien species and unsustainable use of resources (Ceballos and Ortega-Baes 2011). The Equatorial SDF is under severe anthropic pressure (Jara-Guerrero et al. 2019), experiencing a dramatic loss in area in the quality of these forests, exacerbating the biodiversity losses that occurred during the last century, mainly because of agricultural and urban expansion (Mittermeier et al. 1999; Sierra 2013). Originally, 35% of coastal Ecuador was naturally covered with Equatorial SDF, but this ecosystem was reduced to less than 2% by the 1990s (Dodson and Gentry 1991). This alarming situation has catalyzed an effort to protect the last remnants and isolated patches of tropical dry forest (Gentry 1977; Parker and Carr 1992; Best and Kessler 1995; Espinosa et al. 2012; Sierra 2013, Tapia-Armijos et al. 2015). Estimated yearly rate of deforestation in the area was on average of 1.6% between 2000 and 2010 (Sierra 2013). Making matters worse is the fact that the remnants are highly fragmented, reducing their potential of regeneration (Tapia-Armijos et al. 2015). In this context, there is an urgent need for future research evaluating the efficiency of protected areas for the conservation of Equatorial SDF amphibians, under different scenarios of global change.

The level of protection for Equatorial SDF is extremely low (Rivas et al. 2020), less than 5% of its territory being included in nationally protected areas in Ecuador and Peru (Escribano-Avila et al. 2017). To alleviate this aspect, several private entities and local communities are taking steps forward to protect key areas in the region (Escribano-Avila et al. 2017). However, the conservation of this and other ecosystems cannot and should not be the exclusive responsibility of NGOs. The governments of Ecuador and Peru, the civil society of each country (including universities and research centers), and the international community must become more involved in these processes. An essential part of this support is providing the correct information and analysis regarding species distribution, ecology, and status of conservation.

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Competing interests

The authors have declared that no competing interests exist.

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SUPPLEMENTARY INFORMATION

Supplementary Table 1. List of ecosystem types included in the Equatorial seasonally dry forest, based on MAE 2013 and MINAM 2019.

Ecosystem name	**Original name**	**Country**
Jama – Zapotillo Lowland deciduous forest	Bosque deciduo de tierras bajas del Jama – Zapotillo	Ecuador
Jama – Zapotillo Lowland deciduous forest and scurb	Bosque bajo y arbustal deciduo de tierras bajas del Jama – Zapotillo	Ecuador
Jama – Zapotillo Lowland desert scrub	Arbustal desértico de tierras bajas del Jama – Zapotillo	Ecuador
Catamayo – Alamor foothill deciduos forest	Bosque deciduo piemontano del Catamayo – Alamor	Ecuador
Catamayo – Alamor foothill semideciduos forest	Bosque semideciduo piemontano del Catamayo – Alamor	Ecuador
Coastal deciduous shrubland and grassland	Arbustal deciduo y herbazal de playas del litoral	Ecuador
Deciduous forest of the Equatorial Pacific mountain range	Bosque deciduo de cordillera costera del Pacífico Ecuatorial	Ecuador
Anthopical	Intervención	Ecuador
No data	Sin Información	Ecuador
Seasonally dry forest of plains	Bosque estacionalmente seco de llanura	Peru
Seasonally dry forest of hills and mountains	Bosque estacionalmente seco de colina y montaña	Peru
Riverine seasonally dry forest	Bosque estacionalmente seco ribereño	Peru
Algarrobo dry forests	Bosque estacionalmente seco ribereño (Algarrobal)	Peru
Xeric shrublands	Matorral xérico	Peru

Supplementary Table 2. Presence of amphibian species in the provinces (Ecuador) or departments (Peru) throughout the Equatorial seasonally dry forest.

	Ecuador							**Peru**		
Especie	**Loja**	**El Oro**	**Azuay**	**Guayas**	**Santa Elena**	**Manabí**	**Esmeraldas**	**Lambayeque**	**Piura**	**Tumbes**
Rhinella alata		X	X	X						
Rhinella horribilis	X	X	X	X	X	X	X	X	X	X
Hyalinobatrachium tatayoi						X	X			
Ceratophrys stolzmanni	X	X		X	X	X				X
Epipedobates anthonyi	X	X		X					X	X
Epipedobates machalilla		X		X	X	X				
Hyloxalus elachyhistus	X			X				X	X	
Hyloxalus infraguttatus	X	X		X	X	X			X	
Boana pellucens		X	X	X	X	X				X
Boana rosenbergi				X	X	X				
Scinax quinquefasciatus	X	X		X	X	X	X			X
Scinax sugillatus				X						
Scinax tsachila	X	X		X						
Smilisca phaeota		X		X	X	X				
Trachycephalus jordani	X	X		X	X	X	X		X	X
Trachycephalus quadrangulum	X	X		X	X	X	X			
Engystomops guayaco				X						
Engystomops montubio					X	X				
Engystomops pustulatus	X	X		X	X	X		X	X	X
Engystomops puyango	X	X								X
Engystomops randi	X	X	X	X						X
Leptodactylus labrosus	X	X	X	X	X	X	X	X	X	X
Leptodactylus melanonotus				X		X				
Leptodactylus ventrimaculatus	X				X	X	X		X	
Barycholos pulcher	X	X		X	X	X				
Pristimantis achatinus		X	X	X	X	X	X		X	

	Ecuador							Peru		
Especie	**Loja**	**El Oro**	**Azuay**	**Guayas**	**Santa Elena**	**Manabí**	**Esmeraldas**	**Lambayeque**	**Piura**	**Tumbes**
Pristimantis lymani	X	X						X	X	X
Pristimantis subsigillatus		X	X			X				
Pristimantis walkeri					X	X				
Lithobates bwana	X	X		X		X			X	X

CAPÍTULO III

Climate change and distribution expansion of dry forest endemic amphibians: a threat to biological diversity?

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Abstract

Aim: It was studied how vulnerable are the neotropical seasonally dry forests amphibians to climate change. We evaluated the foreseeable changes on their distribution under different IPCC scenarios, defined the vulnerability associated to each amphibian and located where the most vulnerable species are distributed.

Location: The neotropical seasonally dry forests (N-SDF)

Methods: We developed models to evaluate the vulnerability to climate change for 39 amphibian species endemic. To model future conditions, it was considered three global circulation models, each under two Representative Concentration Pathways (RCP) scenarios for greenhouse gas concentration: RCP 4.5 and RCP 8.5 (period 2041-2060). We evaluated the general patterns of change in altitude and directionality between the current and projected suitable areas for each species, as well as the changes in available habitat, analyzed changes in area suitability, and finally assessed species vulnerability to climate change.

Results: The species range expansion will occur under both future climate change scenarios. The new suitable habitats will be located at higher elevations and retain the same percentage of the remaining habitat as the current habitat. We found vulnerability values under 0.5 for the most species. Only four species demonstrated high vulnerability in both RCP scenarios. The Dry Chaco, Chiquitano forest, and Mexico and Central America forests were the nuclei with the highest average vulnerability to climate change

Main conclusions: More than half of the amphibian endemic gained range, in both extension and altitude, under the two climate scenarios suggesting that they could have suitable habitat in the future to colonize, as long as their life-history traits allows it and the vegetation cover is maintained. The changes in patterns of richness by remaining habitat show a gain in the number of species, which implies that species will go from being dispersed to being more concentrated in the future.

KEYWORDS: Distribution models, amphibians, dry forest, climate change scenarios, vulnerability

INTRODUCTION

Climate change is the most dramatic biodiversity threat (Leadley, 2010; Pereira et al., 2010; Thomas et al., 2004). Evidence of massive local extinctions coupled with shifts in species distribution due to cool edge expansion and warm edge contractions are the norm (Burrows et al., 2011; Wiens, 2016). This implies latitudinal (species displacing their ranges to higher latitudes) and elevational (displacing their ranges upslope) (Chen et al., 2011). As a consequence understanding the impacts of climate change on organisms and the sensitivity of each taxonomic group to this global change driver has become a rutinary and indispensable step to guide decision-making for biodiversity conservation and adaptation (Foden & Young, 2016; Moritz & Agudo, 2013).

The recently launched second Global Amphibian Assessment has evaluated more than 8000 species for the International Union for Conservation of Nature (Luedtke et al., 2023). Conclusions are devasting and pose amphibians as the most globally threatened vertebrate class with more than 40 % of them seriously endangered. Deterioration from 2004 draws a dramatic situation with climate change overpassing disease and habitat loss concerns in the recent past (Stuart et al., 2004).

Amphibian diversity together with the rest animal diversity of seasonally dry forests in the Neotropics remains poorly studied (Sánchez-Azofeifa et al., 2005). Although a clear trend to lower species richness in comparison with more humid biomes such as rainforests and cloud forests is a norm (Guedes et al., 2018; Hanson et al., 2010; Jenkins et al., 2013), there is no doubts that its relevance at the global scale is unquestionable (Armijos-Ojeda et al., 2021). Recent evidence points out the existence of high levels of amphibian endemicity and a panoply of outstanding adaptations to face long periods of food scarcity and water stress (Chazdon et al., 2011; Stoner & Timm, 2011). If our knowledge on the amphibian diversity of seasonally dry forests is low, its response to oncoming warming is almost null in spite of the dramatic deforestations rates and the pervasive action of other Global Change drivers such as overgrazing and contamination (Luedtke et al., 2023).

The first step in the development of any effective management and conservation strategy for amphibians is the completion of regional inventories, especially in the context of rapid biodiversity loss and climate changes. Understanding species distribution is especially urgent in the case of amphibians, the most threatened vertebrate group worldwide

(Catenazzi et al., 2014). In this context, our aim was to update the list of amphibian species and their distribution in the coastal SDF of Ecuador and Peru, through extensive fieldwork and the compilation of all available information, to prioritize conservation actions, promote public awareness and focus further inventory efforts towards areas where gaps remain.

Climate change vulnerability assessment is probably one of the most efficient tool to deal with this critical necessity (Arribas et al., 2012; Pacifici et al., 2015; Souza et al., 2023; Still et al., 2015). Species vulnerability is defined as the susceptibility of a species to show a negative demographic response to environmental alterations, for instance climate change (Smit et al., 2000). It depends on a combination of extrinsic and intrinsic factors such as the sensitivity, adaptative capacity and degree of exposure to climate change (Pacifici et al., 2015; Still et al., 2015; Williams et al., 2008). Species distribution models (SDMs) are widely used to define species vulnerability evaluating foreseeable climate change scenarios (Mateo et al., 2011; Willis et al., 2015) and taking into consideration the action of other drivers of Change together with some idiosyncratic features of each species such as particular ecological requirements and/or low dispersal capabilities (Nowakowski et al., 2017; Székely et al., 2018). Although amphibian distribution under climate scenarios depends not only on the predicted oncoming conditions, but also on some endogenous features of species, such as dispersal capacity, biotic interactions (competition, predation, symbiosis with other species), landscape structure (natural barriers and habitat fragmentation) and adaptability to new conditions (Davis et al., 1998; Mateo et al., 2011; Pearson & Dawson, 2003), SDMs are a valuable tool for understanding responses, especially for species with narrow distribution (Gibson et al., 2010) or that inhabit threatened ecosystems (Milanovich et al., 2010).

We build climate models for a complete set of amphibians, endemic to the neotropical seasonally dry tropical forests. These amphibians share two crucial features than make extrapolation from other relatives from humid regions very difficult: i) their eco-physiological achievements that enable them to adapt a habitat with prolonged and severe water deficits (Aguillón, 2018; Corn, 2005; Duellman, 1988; Schivo et al., 2019; Stan & Sanchez-Azofeifa, 2019) such as permeable skin, complex life cycles, unshelled eggs and ectothermic physiology (Duellman & Trueb, 1994), and ii) their confinement to one of the most endangered ecosystems in the world, where almost 60% of their original extent has been destroyed and the remaining is characterized by habitat fragmentation and degradation (Portillo-Quintero & Sánchez-Azofeifa, 2010).

Amphibians are deeply affected by global warming (Blaustein et al., 2003) because they are particularly vulnerable to changes in temperature and precipitation (Cayuela et al., 2012; Kiesecker et al., 2001; Lawler et al., 2010). There is some evidence of direct climate change effects (Lawler et al., 2010), mostly associated with outbreaks of emerging diseases (D'Amen & Bombi, 2009; Daszak et al., 2003), and embryo mortality by ultraviolet radiation (Kiesecker et al., 2001). Alterations of the reproductive cycle, early stage development, foraging and hibernation patterns due to climate change are also described (Donnelly & Crump, 1998; Li et al., 2013; Parmesan, 2007). Latitudinal and altitudinal shifts in response to the new climatic conditions are frequent for most amphibians resulting in either reduction, displacement, and increase in their geographic range, depending on the species requirements and resilience (Schivo et al., 2019). It is widely accepted that this animal group is experiencing a steep decline which should be exacerbated in the future as a consequence of warming (Corn, 2005) and the simultaneous action of other drivers of Global Change (Beebee & Griffiths, 2005). Unfortunately, our knowledge on the warming responses and adaptation of those amphibians that inhabit seasonal dry forests is almost null. Even more, extrapolation from the responses of amphibians inhabiting rain and cloud forests is not recommendable since phenotypic achievements and ecological responses are critically different (Silva Souza et al., 2023). With this in mind, we have evaluated how vulnerable are the neotropical seasonally dry forests amphibians to climate change. Specifically, we have evaluated the foreseeable changes on their distribution under different IPCC scenarios, defined the vulnerability associated to each amphibian and located where the most vulnerable species are distributed.

METHODS

Study area

The neotropical seasonally dry tropical forests (N-SDF) are confined in the Americas between the Tropic of Cancer (23.5°N) and the Tropic of Capricorn (23.5°S) (Wright et al., 2009). They are characterized by a relatively long period lasting at least five or six months with less than 100 mm of precipitation. Vegetation is dominated by semi deciduous and deciduous trees (Linares-Palomino, 2004; Miles et al., 2006; Pennington et al., 2000). These forests are considered as one of the most endangered ecosystems worldwide, since about 60% of the original forest has already disappeared and the remnants are very degraded (Miles et al., 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010; Sánchez-Azofeifa et al., 2011).

Limits of the N-SDF were based on the map of world terrestrial ecoregions proposed by The Nature Conservancy (TNC) (http://maps.tnc.org/gis_data.html) (see Appendix S1). We selected and classified the ecoregions defined as N-SDF according to the biogeographic nucleus proposed by Pennington et al. (Pennington et al., 2000). The resulting classification is shown in Figure 1 (see Appendix S1).

FIGURE 1. Distribution of the biogeographic nuclei in the Neotropical seasonally dry forests.

Species occurrence data

For the selection of focal species, we followed the IUCN Red List of amphibians (IUCN, 2023) including only those amphibian species whose distribution was restricted to the N-SDF. We conducted a comprehensive search using online databases, scientific articles, and private and institutional biological collections to obtain occurrence records (see Appendix S2). We standardized the names according to the system proposed by Frost 2023 to ensure accuracy.

Occurrence data curation

The data curation process followed the methodology proposed by Hijmans and Ellith (2013), which involved four steps. First, data with typographical errors in the coordinates or values that indicate no data were eliminated. Second, duplicate records were removed. Third, records whose coordinates did not correspond to the registered country were eliminated. Finally, a single record was selected per pixel of 30 seconds of arc (~1 km) to reduce sampling bias. Data curation was carried out using the R package Dismo (Hijmans et al., 2017). Finally, we retained for further modelling those species with at least 14 occurrences.

Environmental data

We selected 19 variables from Climatologies at high resolution for the earth's land surface areas - CHELSA (Karger et al., 2017) (https://chelsa-climate.org/). These variables have a spatial resolution of 30 arcseconds (~1 km). To predict responses under oncoming conditions, we used three global circulation models: GFDL-CM3(Gordon & Stern, 1982), HadGEM2-CC (Hewitt et al., 2011) y MPI-ESM-LR (Giorgetta et al., 2011), each one under two Representative Concentration Pathways (RCP) scenarios for emissions of the IPCC: RCP 4.5 (low-medium emissions) and RCP 8.5 (high emissions) (Raghavan et al., 2019), corresponding to the 2041-2060 period.

Species distribution models

In order to avoid multicollinearity problems we conducted a Pearson correlation analysis ($r \leq -0.8$) to select predictors (Ortega-Andrade et al., 2021). Then we made a jackknife test to select the four or five variables that exhibited the highest permutation importance while also lacking correlations (Nori et al., 2011) (see Appendix S3). Final models were created and evaluated using the kuenm R package, which uses the MaxEnt 3.4.4 algorithm and presence-only data to determine the spatial distribution area for each species (Phillips et al., 2006). We used 75% of the data for training models and 25% for testing the models. To calibrate the models, we generated candidate models by combining five to six distinct sets of environmental variables, six regularization multiplier settings (0.1, 0.25, 0.5, 1, 2, 4), and seven response types, including linear (l), quadratic (q), product (p), as well as their combinations (lq, lp, qp, lqp) (see Appendix S3 for more details). Based on the "BAM" diagram (Soberon & Peterson, 2005), we considered as calibration area “M” (accessible area with adequate conditions for species occurrence) an area of 10 km around the biogeographic nucleus (Figure 1). We evaluated the performance of the candidate models based on several criteria, including partial ROC (with 500 iterations and 50% of the data for bootstrapping), omission rates (E = 5%), and model complexity (AICc). We selected models with omission rates ≤ 5% and delta AICc ≤ 2 (Cobos et al., 2019; Raghavan et al., 2019) (see Appendix S4 for further details). The final models were generated based on calibrated models projected for the period 2041-2060 using 5 replicates. For the projection we defined a buffer area of 50 km around each “M” calibration. We obtained a result for each General Circulation Model (GCM), Representative Concentration Pathway (RCP), and type of extrapolation (without extrapolation, free extrapolation, and extrapolation with clamping). The output format used was the cloglog transformation, which has a better theoretical justification than the logistic transformation (Phillips et al., 2017). To quantify the model uncertainty associated with extrapolation, Maxent uses Multivariate Environmental Similarity Surface (MESS) index (Elith et al., 2010). The species distribution models show the changes in suitable areas considering all GCMs. For our study, we considered as: 0) unsuitable – areas with no suitability for the current period and for all GCMs; 1) gain areas – the areas which are currently not suitable, but gain suitability under all three GCMs; 2) loss areas – the areas which are currently suitable but will lose suitability under the three GCMs; 3) stable areas – the areas that are suitable in the present and remain suitable under all future GCMs.

Remaining habitat data

The information of remaining habitat was obtained for the year 2019 from Copernicus Global Land Cover Layers – Collection 2 (100 m resolution) (Buchhorn et al., 2020) available in https://lcviewer.vito.be/2019. We selected as remnant suitable vegetation the classes that correspond to forests (codes 111 – 116, 121 – 126) and shrubland (code 20).

Projected changes in species spatial distribution

To evaluate the changes in species spatial distribution we obtained a map of Projected suitable area for the species under the two RCPs by adding the surface in the category "stable areas" and the surface in the category "gain areas". We evaluated the patterns of changes, considering the changes in altitude and direction (latitude and longitude) between the present suitable areas and the projected suitable areas. We used the GTOPO30 global digital elevation model (Miliaresis & Argialas, 1999) (available at https://earthexplorer.usgs.gov/) with a spatial resolution of 30 arc sec to calculate the changes in altitude. We extracted the lower, upper and mean altitude for present and projected suitable areas for each species under the two RCPs. We calculated the change in the angle and distance between the present suitable area centroid and the projected "gain area" centroid as a measure of direction change. To summarize the aggregation and directional results we grouped the species into three geographical zones: Central America (Mexico and Central America), South America (Pacific coastal Ecuador and Peru, Dry Chaco, Chiquitano, Caatinga, Cerrado) and the Caribbean (Caribbean coast of Colombia and Venezuela, Colombian Interandean valleys, Antilles) and analyzed these with the functions rho.circular and rayleigh.test from the "circular" package (Lund et al., 2017). We considered as high aggregation the values close to 1 and as high disaggregation the values close to 0. Additionally, for each species we evaluated the changes in available habitat between present and future considering a conservative scenario in which vegetation is maintained. Afterwards, to better understand the species response to climate change we analyzed the changes in area suitability. For this, we used the three indicators proposed by Still et al.(2015) which are: 1) *Change in suitable area*, 2) *Suitable area overlap* and 3) *Suitability score*.

The *change in suitable area*, defined as the amount of contraction or expansion between the surface in the present suitable area (t1) and the projected suitable area (t2) was calculated using the Equation 1.

Equation 1.

$$\text{Change in suitable area} = [(\text{Area}_{t2} - \text{Area}_{t1}) / \text{Area}_{t1}] \times 100$$

Values range between -1 (when all the suitable surface for the species in the present disappeared in the future projection) to > 1 (when the suitable area increases in the future). We classified the *Change in suitable area* results into five categories: High loss (-1 ≤ *change suitable area* < - 0.50), Loss (- 0.50 ≤ *change suitable area* < - 0.05), Stable (- 0.05 ≤ *change suitable area* < 0.05), Gain (0.05 ≤ *change suitable area* < 0.50) and High gain (*change suitable area* > 0.50).

The percentage of suitable area that overlaps between present (t1) and future (t2) was calculated using the Equation 2.

Equation 2.

$$\text{Suitable area overlap} = \ [(\text{Overlap between Area}_{t1} \text{ and Area}_{t2}) \ / \ \text{Area}_{t1}]$$

Values range between 0 (when there is not overlap in suitable area between present and future) to 1 (when the entire area suitable in the present will remain suitable in the future). According to Still et al.(2015), low values of suitable area overlap could show that suitable area is predicted to contract or shift in the future. We classified *Suitable area overlap* into four categories: Not overlap (*suitable area overlap = 0)*, Low overlap (0 < *suitable area overlap* < 0.5), Medium overlap (0.5 ≤ *suitable area overlap* < 0.75), High overlap (0.75 ≤ *suitable area overlap* ≤ 1).

The third indicator is the change in climatic suitability between the present area and the projected suitable area. Unlike the formula proposed by Still et al.(2015), we use the values of all pixels included in the species present distribution area as shown in Equation 3.

Equation 3.

$$\text{Suitability score} = \text{Mean}((\text{Suitability}_{t2} - \text{Suitability}_{t1}) \ / \ \text{Suitability}_{t1})$$

This score ranges between -1 to 1, the negative values indicate that the average suitability in the present area is predicted to decrease in the future and the positive values indicate that the average suitability in the present area is predicted to increase. We classified *Suitable score* into five categories: High loss (-1 ≤ *suitability score* < - 0.25), Loss (- 0.25 ≤ *suitability score* < - 0.05), Stable (- 0.05 ≤ *suitability score* < 0.05), Gain (0.05 ≤ *suitability score* < 0.25) and High gain (0.25 ≤ *suitability score* ≤ 1).

Additionally, we analyzed the changes on spatial species accumulation in each biogeographic nucleus adding the suitable areas of each species for each biogeographic core. Then, to represent the change in richness in the future compared to the present, we calculated a rate of change in richness under the two RCPs with the Equation 4:

Equation 4.

$$Change\ in\ richness: \frac{(Richness_{t2} - Richness_{t1}) * 100}{Richness_{t2}}$$

where Richness$_{t1}$– present species richness, Richness$_{t2}$– future species richness.

Values range between -100 to 100, the negative values indicate the loss of richness and positive values indicate the predicted gain in richness. We classified *Change in richness* into five categories: High loss (-100 ≤ *change in richness* < - 50), Loss (- 0.50 ≤ *change in richness* < - 5), Stable (- 5 ≤ *change in richness* < 5), Gain (5 ≤ *change in richness* < 50) and High gain (50 ≤ *change in richness* ≤ 100).

Vulnerability analysis

It is known that species vulnerability depends on both external and intrinsic factors (Williams et al. 2008). Here we evaluated the vulnerability only in response to external factors, such as climate change and land use change; however, if the displacement occurs towards areas lacking natural habitat or the level of degradation is very high, the performance and survival of the species could still be threatened independently of the climate suitability. So, we consider that in such cases the species can hardly gain the predicted expansion of the habitat.

For this, we used two indicators proposed by Maggini et al. (2014), one by Still et al. (2015) and fourth from our side to evaluate the projected change in distribution. The values of each indicator range between 0 (no contribution to vulnerability) and 1 (maximal contribution).

The first indicator (*IAO*) uses the present suitability area (t1) and the projected suitability area (t2) to measure the relative amount of change that is projected under the two RCPs (Equation 5).

Equation 5.

$$\text{IAO} = \frac{(AO_{t1})}{AO_{t1} + AO_{t2}}$$

The second indicator (*IOverlap*) considers the relative overlap between present suitability area (t1) and the projected suitability area (t2) (Equation 6).

Equation 6.

$$\text{IOv} = 1 - (\frac{Overlap}{AO_{t1}})$$

The third indicator (*Is*) measures the relative difference for the suitability between present suitability (t1) and the projected suitability (t2) (Equation 6).

Equation 7.

$$\text{Is} = 1 - \left(\frac{S\text{uitability score} + 1}{2}\right)$$

The last indicator (*IAOr*) measures the available habitat under the two RCPs, relating the remaining habit in the present (t1) with the remaining habitat in future (t2) (Equation 8).

Equation 7.

$$\text{IAOr} = 1 - \left(\frac{AOr_{t1}}{AOr_{t2}}\right)$$

The four indicators were combined to obtain a Vulnerability Index

Equation 8.

$$\text{IAOr} = \frac{\frac{\text{IAO} + \text{IOv}}{2} + \text{IAOr} + \text{Is}}{2}$$

We classified the Vulnerability Index (*IAOr*) into three categories: Low vulnerability (0 ≤ *IAOr* < 0.34), Medium vulnerability (0.34 ≤ *IAOr* < 0.67), and High vulnerabiliy (0.67 ≤ *IAOr* ≤ 1).

Finally, we spatialize the vulnerability index for the N-SDF calculating the average vulnerability per pixel, that is, the sum of the vulnerability index obtained for each species present in each pixel divided by the total number of species present in that pixel. The resulting values were classified into three categories: Low vulnerability ($0 \leq IAOr < 0.34$), Medium vulnerability ($0.34 \leq IAOr < 0.67$), and High vulnerability ($0.67 \leq IAOr \leq 1$).

RESULTS

Species distribution models

A total of 76 species of amphibians were identified as endemic for the N-SDF, of which we retained the 39 species that have the minimum occurrence records (14) required for modelling. We generated a total of 5568 candidate models for the selected species, of which 1739 models met the omission rate criteria, 113 models met the AICc criteria, and 78 models corresponding to 30 species met both criteria, the omission rate and AICc (see Appendix S3). The models for the remaining nine species (all of them with a minimum of 30 occurrence records) met only one of the criteria but were included in the analysis for their importance from a conservation and adaptation perspective. For more details about evaluation parameters and environmental variables used in the selected models for each species see Appendix S3 y S4.

Projected changes in species spatial distribution

Our results indicate changes in the elevational ranges in the evaluated future scenarios (Figure 2). More than a half of species showed an increase in their upper elevational limit (51% and 53% for RCP 4.5 and RCP 8.5, respectively). On the other hand, only 13% of species in the RCP 4.5 and 10% of species under RCP 8.5 reduced their upper elevational limit, while the remaining species maintained their upper elevation. Regarding the changes in the lower limit, about 82% of species maintained their lower elevation limit under the two RCPs, while less than 10% of species changed under the two RCPS (Figure 2). Overall, more than the 50% of species expand their spatial ranges and only few species maintained or contracted their spatial ranges.

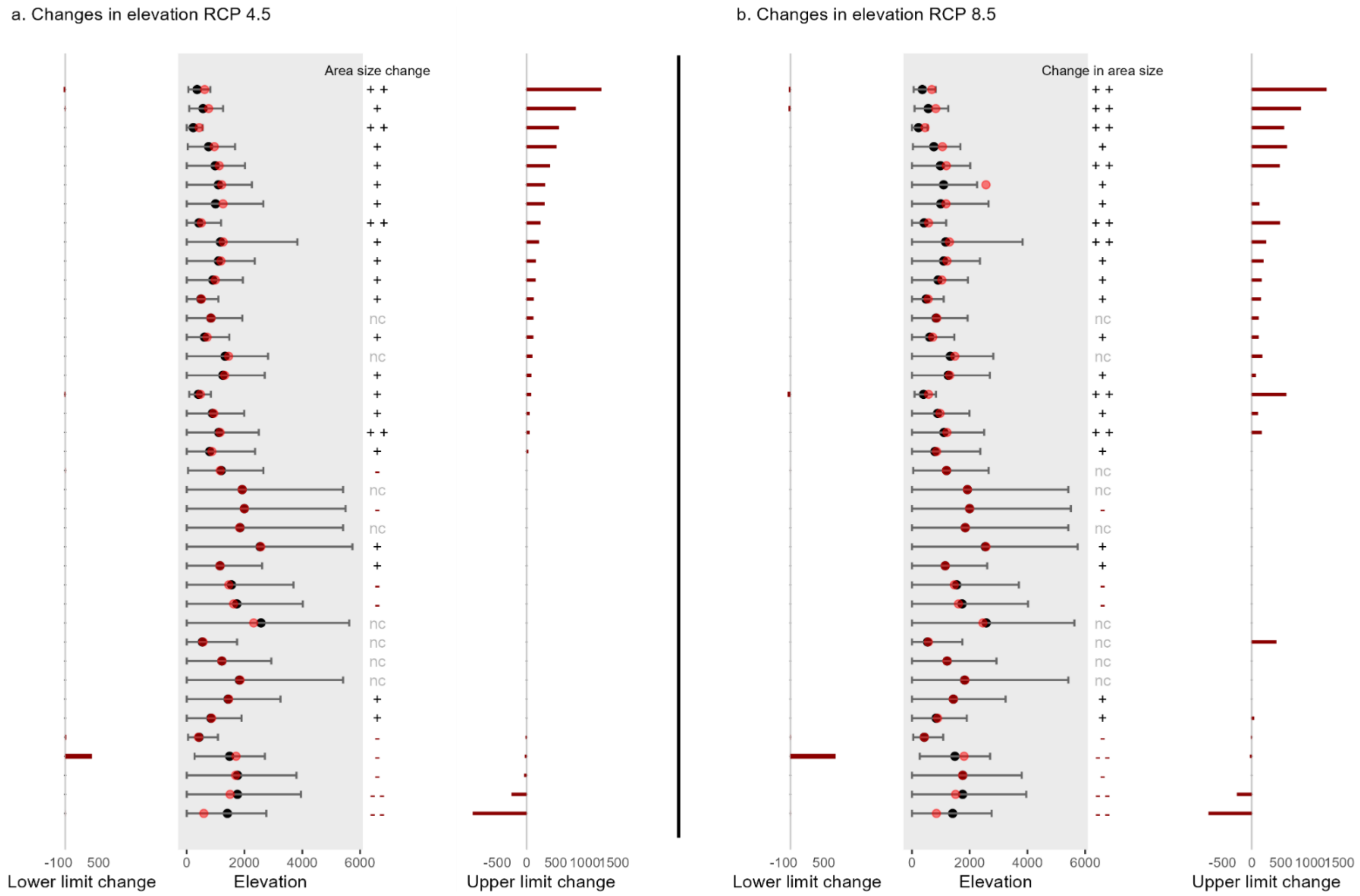

FIGURE 2. Changes in elevation or the 39 endemic amphibians of N-SDF, under two climate change scenarios (RCP 4.5 and 8.5). For each species, the black dots represent the present mean elevation, and the red dots represent the mean elevation in the future. The lower and upper limit of the elevation range for each species are represented as whiskers, while the sidebar graphs show whether these limits increased, be maintained or decreased. The change in area size is indicated by (+) and (-) signs [--: High loss, - Loss, nc: no change: +, Gain: ++, High gain].

When we analyzed the direction of expansion of the spatial ranges in each biogeographical zone, we did not find a specific directional pattern of movement, nor a pattern of centroid aggregation under the two RCPs (see Fig. 3 and Appendix S5).

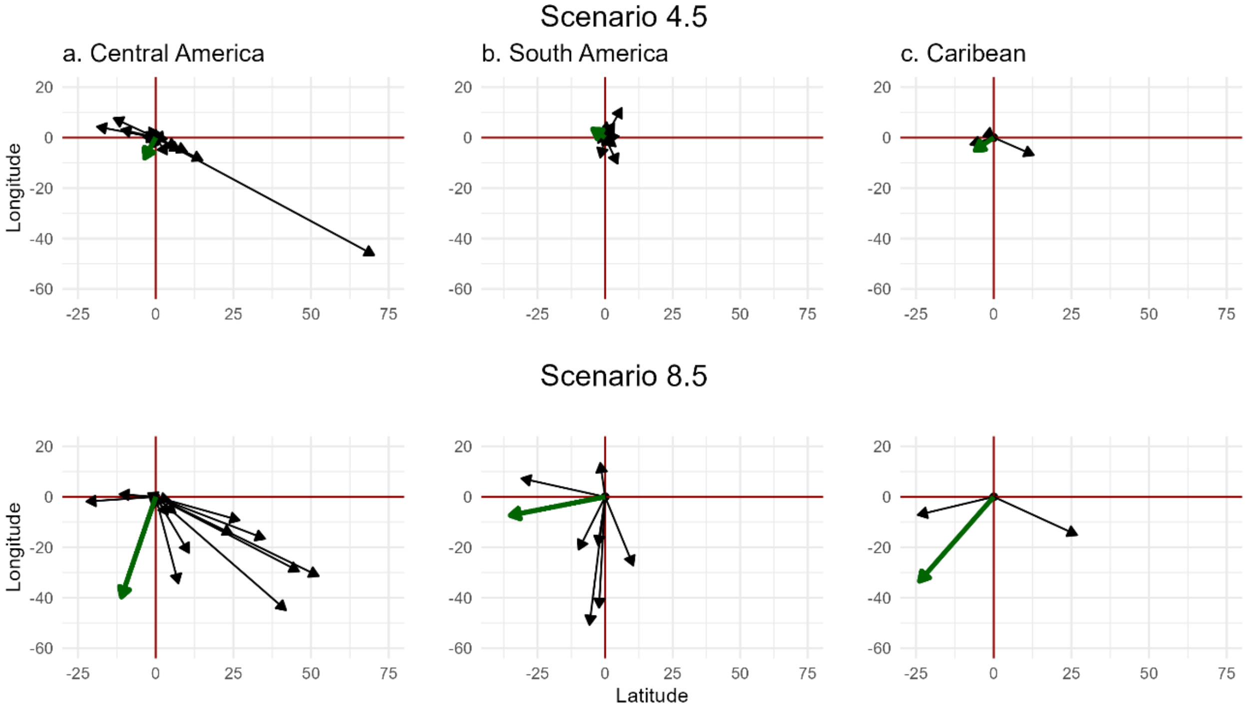

FIGURE 3. Direction of change in spatial range for the endemic species under two climate change scenarios (RCP´s 4.5 y 8.5), grouped into the three biogeographic zones: (a) Central America (Mexico and Central America), (b) South America (Pacific coastal Ecuador and Peru, Dry Chaco and Chiquitano, Caatinga – Cerrado) and (c) Caribbean (Caribbean coast of Colombia and Venezuela, Colombian InterAndean valleys, Antilles).

The proportion of remaining vegetation within species' distribution ranges remained consistent between current and projected suitable areas (See Appendix S6) (without considering land cover changes that may occur in the future). Only for two species under the RCP 4.5 and two species under the RCP 8.5 the projected suitable area will lose more than the 50% of remaining habitat. Thus, for the species *Lithobates pustulosus* (Boulenger, 1883), only the 40% (approximately) of their projected suitable area will have natural vegetation under the two RCP scenarios. The same occurs with *Leptodactylus laticeps* (Boulenger, 1918), for which about of 30% of their projected suitable area would have adequate vegetation under the RCP 8.5 scenario. Finally, in the case of *Exerodonta xera* (Mendelson and Campbell, 1994), 7% of the projected suitable area will be covered with natural vegetation under RCP 4.5, although the observed pattern would be different under the RCP 8.5 scenario (Figure 4).

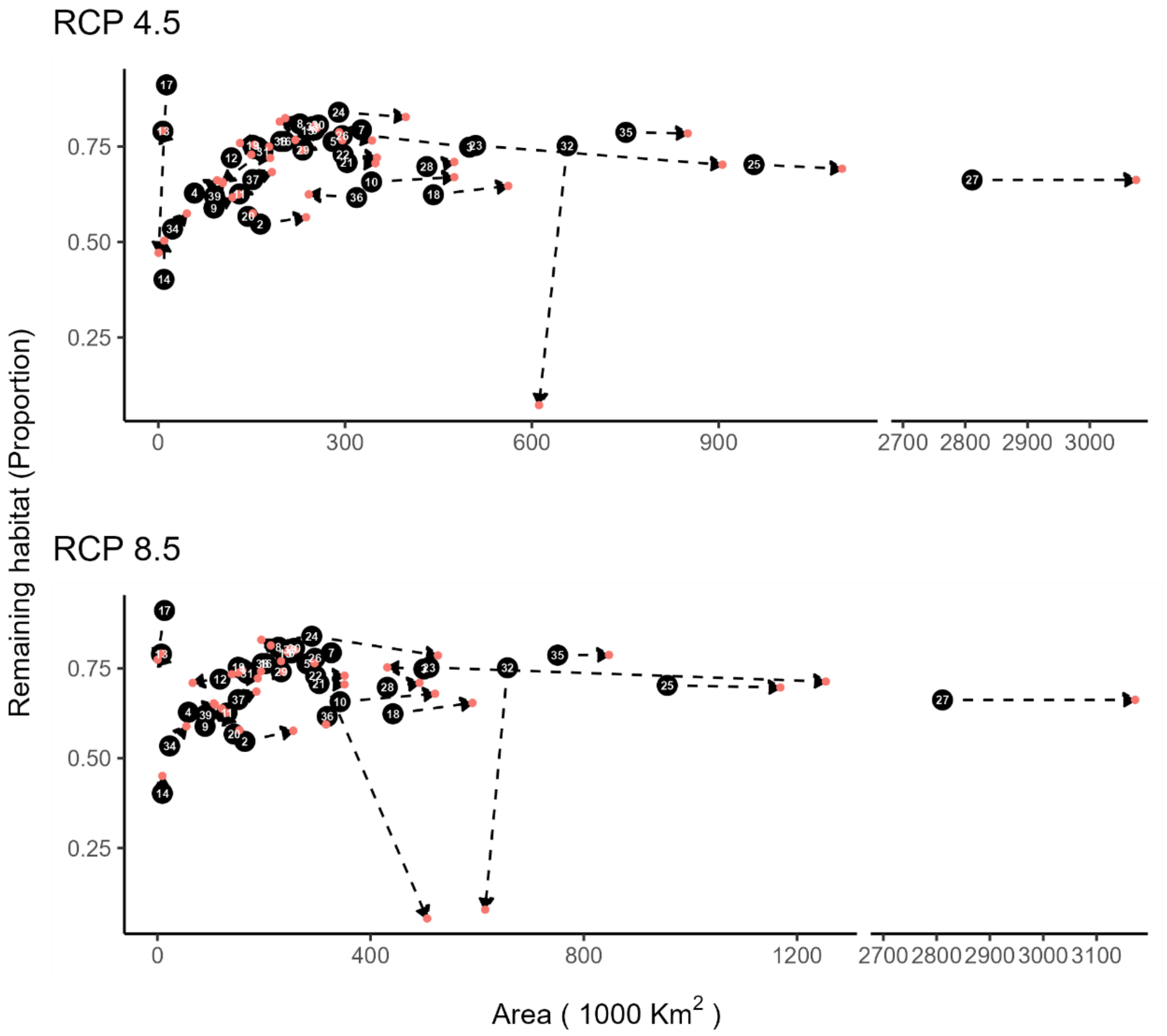

FIGURE 4. Changes in remaining habitat between present and projected suitable areas for the endemic amphibians of the N-SDF. The black dots represent the proportion of remaining vegetation in the present suitable area and the red dots represent the proportion of remaining vegetation in the future projected suitable area under two scenarios of climate change (RCP 4.5 and RCP 8.5). Species codes: (1) *Agalychnis dacnicolor*, (2) *Ceratophrys calcarata*, (3) *Ceratophrys cranwelli*, (4) *Ceratophrys stolzmanni*, (5) *Craugastor hobartsmithi*, (6) *Craugastor occidentalis*, (7) *Craugastor rugulosus*, (8) *Craugastor vocalis*, (9) *Dendropsophus robertmertensi*, (10) *Dendropsophus sartori*, (11) *Eleutherodactylus atkinsi*, (12)

Eleutherodactylus modestus, (13) *Engystomops puyango,* (14) *Engystomops randi,* (15) *Exerodonta smaragdina,* (16) *Exerodonta sumichrasti,* (17) *Exerodonta xera,* (18) *Incilius canaliferus,* (19) *Incilius gemmifer,* (20) *Incilius luetkenii,* (21) *Incilius marmoreus,* (22) *Incilius perplexus,* (23) *Lepidobatrachus laevis,* (24) *Lepidobatrachus llanensis,* (25) *Leptodactylus bufonius,* (26) *Leptodactylus laticeps,* (27) *Leptodactylus latrans,* (28) *Lithobates forreri,* (29) *Lithobates magnaocularis,* (30) *Lithobates megapoda,* (31) *Lithobates neovolcanicus,* (32) *Lithobates pustulosus,* (33) *Lithobates zweifeli,* (34) *Peltophryne guentheri,* (35) *Pleurodema tucumanum,* (36) *Pleurodema diplolister,* (37) *Smilisca fodiens,* (38) *Tlalocohyla smithii,* (39) *Triprion spatulatus.*

Most N-SDF areas would maintain the species diversity patterns (Figure 5). Less than 20% of the surface would experience a loss of richness under either of the two scenarios, whereas over 25% of N-SDF area would show a high gain of species richness, specially under 8.5 RCP scenario.

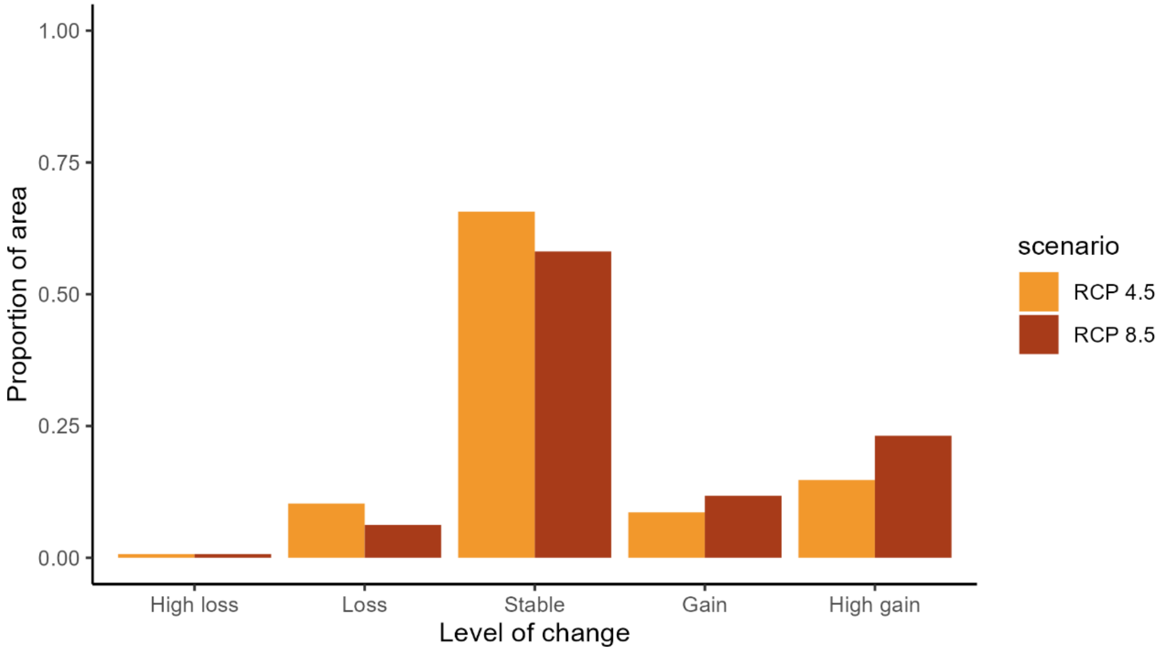

FIGURE 5. Changes in endemic amphibians richness for the neotropical seasonally dry forests, under two climate change scenarios, RCP 4.5 and 8.5. [High loss (-100 ≤ change in richness < -50), Loss (- 0.50 ≤ change in richness < - 5), Stable (- 5 ≤ change in richness < 5), Gain (5 ≤ change in richness < 50) and High gain (50 ≤ change in richness ≤ 100)].

Changes in area suitability

In general, the largest number of species showed a gain in the area of suitable habitat between present and future projections, specially under the 4.5 RCP scenario (Figure 6a). Also, there is a high overlap (Figure 6b) between the present and projected suitable areas under both RCP scenarios for more than the 75% of species, which means that many of the suitable areas in the present continue to be suitable in the future and expands. An increase in suitability for the projected areas can also be observed and less than 25% of species show a decrease in the suitability values for the projected distribution areas under either RCP scenarios (Figure 6c).

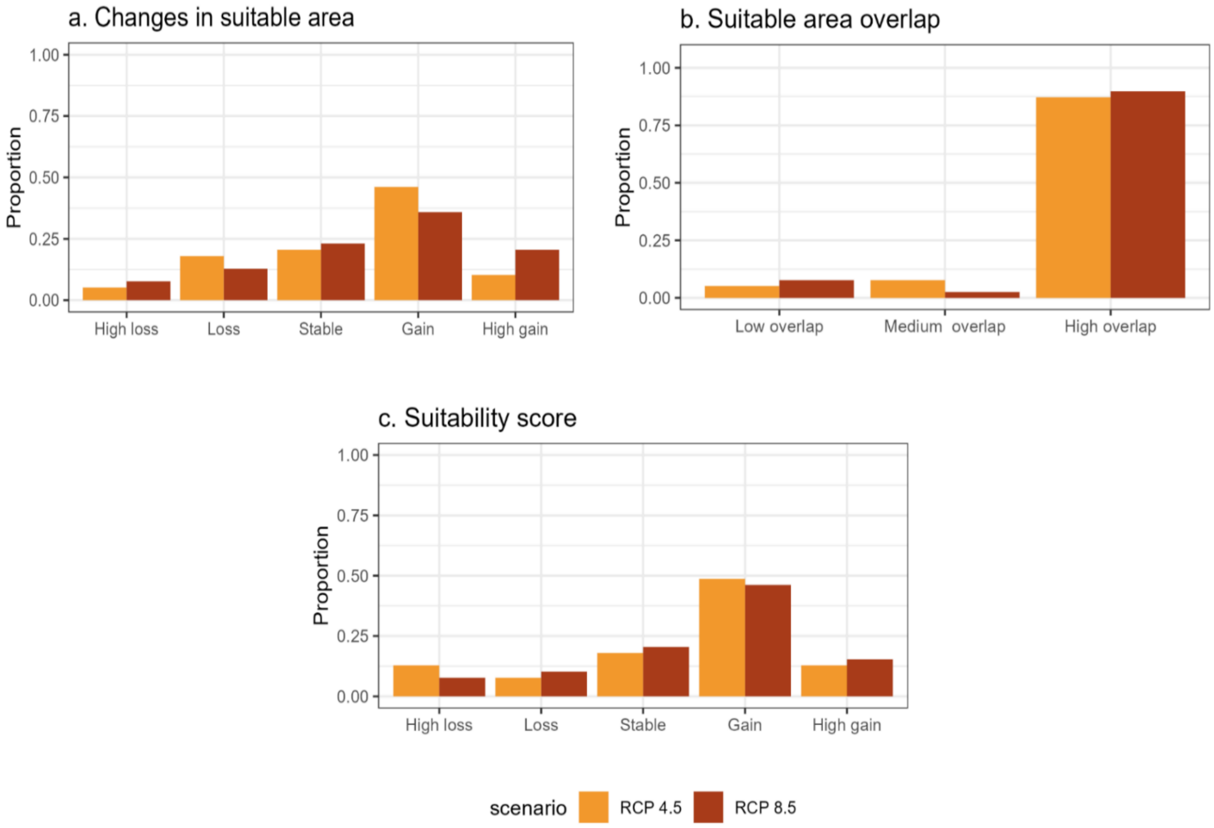

FIGURE 6. Change in area suitability for 39 amphibian species endemic to the N-SDF, under two climate change scenarios, RCP 4.5 and RCP 8.5 **(a) Change in suitability area** (Values for change in suitable area: High loss (-1 ≤ *change suitable area* < - 0.50), Loss (- 0.50 ≤ *change suitable area* < - 0.05), Stable (- 0.05 ≤ *change suitable area* < 0.05), Gain (0.05 ≤ *change suitable area* < 0.50) and High gain (*change suitable area* > 0.50) ; **(b) Suitable area overlap** (Values for Suitable area overlap: Not overlap (suitable area overlap = 0), Low overlap (0 < suitable area overlap < 0.5),

Medium overlap ($0.5 \leq$ suitable area overlap < 0.75), High overlap ($0.75 \leq$ suitable area overlap ≤ 1) ; **(c) Suitability score** (Values for Suitability score: High loss ($-1 \leq$ suitability score < -0.25), Loss ($-0.25 \leq$ suitability score < -0.05), Stable ($-0.05 \leq$ suitability score < 0.05), Gain ($0.05 \leq$ suitability score < 0.25) and High gain ($0.25 \leq$ suitability score ≤ 1).

Vulnerability analysis

Vulnerability analyses (Figure 7) showed that the largest number of N-SDF amphibians presented a medium vulnerability (31% under 4.5 RCP and 82% under 8.5 RCP). In the 4.5 RCP scenario the highest number of species (approximately 70%) presented a low vulnerability. However four species of the dry forests of Mexico and Central America, *Exerodonta xera* (Mendelson and Campbell, 1994) which presented high vulnerabilty under the two scenarios and *Craugastor rugulosus* (Cope, 1870), *Lithobates neovolcanicus* (Hillis and Frost, 1985) and *Lithobates pustulosus* (Boulenger, 1883) were highly vulnerable under the 8.5 RCP scenario.

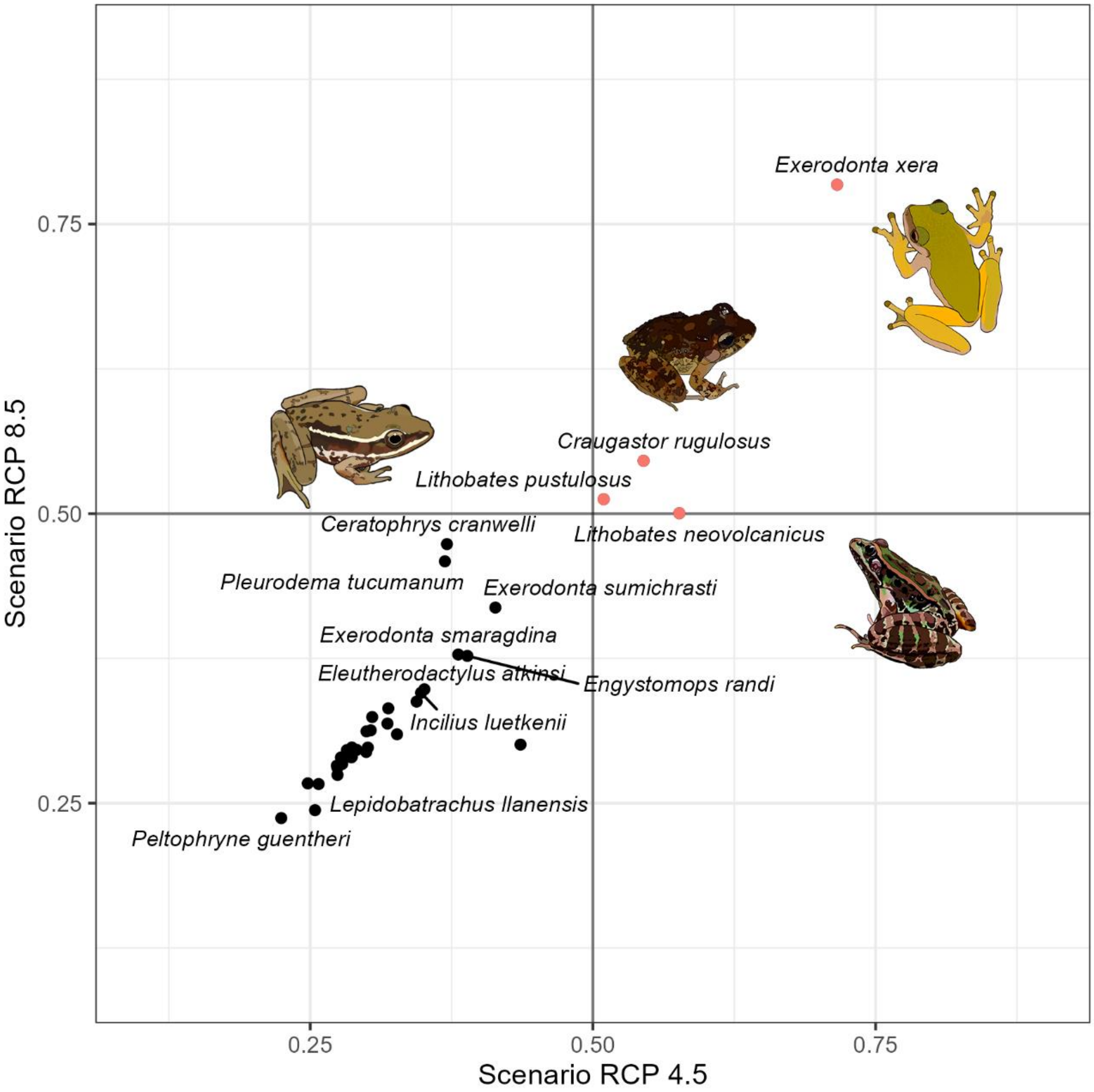

FIGURE 7. Vulnerability index for 39 amphibians of the N-SDF, under two climate change scenarios, RCP 4.5 and RCP 8.5. (Values for Low vulnerability: Low vulnerability ($0 \leq IAOr < 0.34$), Medium vulnerability ($0.34 \leq IAOr < 0.67$), High vulnerability ($0.67 \leq IAOr \leq 1$). Red dots show the species with high vulnerability.

For the two projected scenarios the higher values of mean vulnerability are concentrated in the Dry Chaco and Chiquitano dry forest nucleus, followed by Mexico and Central America dry forests, where the highest values are concentrated in the dry forests of central western Mexico (Figure 8). Under the 8.5 RCP, there are additionally high values of mean vulnerability for the species from the Caribbean Coast of Colombia and Venezuela (Figure 8).

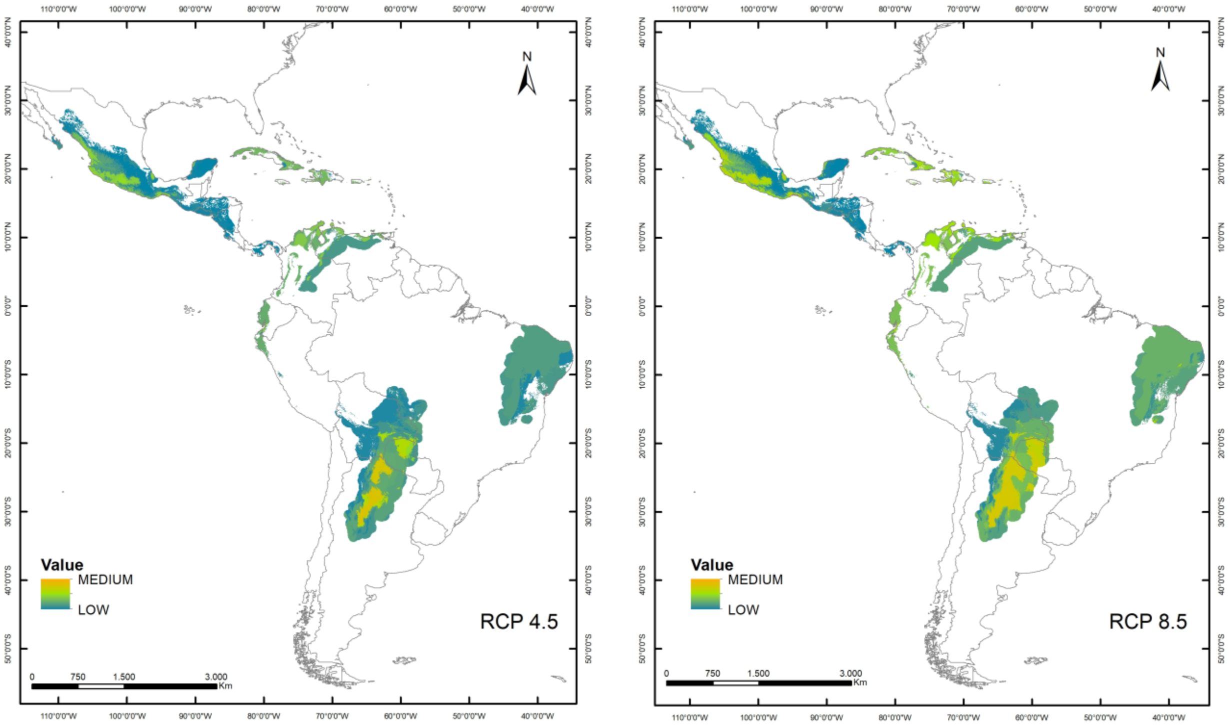

FIGURE 8. Spatial distribution of mean vulnerability values for the N-SDF amphibian endemic species under RCP 4.5 and RCP 8.5 climate change scenarios (Low vulnerability: $0 \leq IAOr < 0.34$) [blue color]), Medium vulnerability: $0.34 \leq IAOr < 0.67$ [orange color], High vulnerability: $0.67 \leq IAOr \leq$ [red color]).

DISCUSSION

Amphibians have been recently recognized as the most threatened vertebrate group (Luedtke et al., 2023) with large-scale and non-random massive declines occurring especially in the Neotropics (Pounds et al., 2006; Pounds, 2001; Stuart et al., 2004; Thomas et al., 2004), where climate change has overpassed disease and habitat loss as the main drivers of this biodiversity loss. However, available information on the status and climate change concern of the very valuable group of amphibians occurring in the seasonal dry forests of the Neotropics is lacking (Armijos-Ojeda et al., 2021), in spite of the fact that N-SDF are considered one of the most threatened ecosystems worldwide (Ferrer-Paris et al., 2019). This is especially demanding since these ecosystems shelter a high level of amphibian endemicity (Luna-Gómez et al., 2017). Even more extrapolation of adaptation and mitigation measures from amphibians restricted to more humid forest ecosystems is limited since adaptations to face long periods of food scarcity and water stress make the difference (Beebee & Griffiths, 2005). Here, we evaluated the vulnerability to climate change in 39 endemic amphibians of the N-SDFs. We used current ecological niches to predict their foreseeable shifts in the geographic ranges (Hannah et al., 2007; Still et al., 2015).

Our results clearly challenge our expectations of a generalized negative effect based on the abundant evidence on the topic (Ballesteros-Barrera et al., 2022; Garcia et al., 2014; Thomas et al., 2004), Surprisingly, we found that most amphibians have medium or low vulnerability to climate change under 4.5 and 8.5 RCP, and only four species from 39 have high vulnerability. For most amphibians of N-SDFs, we found increases in available potential bioclimatic envelopes coupled with the existence in the projected areas of suitable natural vegetation remnants.

Most species will experience an expansion of their geographical range, primarily to upslope areas. Moreover, many species are expected to maintain their current distribution, specifically retaining the lower limits of their range, and the projected areas are also going to increase in habitat suitability, implying that most amphibians will have more available habitat. As Earth's temperature rises, it is likely that species adapted to dry environments and high temperatures will extend their distribution into regions that will, in the future, resemble their original habitat conditions due to climate change (Araújo et al., 2006). This pattern has also been observed for example in birds and plants, where predictions showed the species range expansion and the migration of dry forest communities towards higher elevations (Prieto-Torres et al., 2016). Worth to note that our study considered a buffer area of 50 km, assuming that amphibians are capable of dispersal to new areas over such a distance over the projected time- frame. However, due to their restricted distribution ranges and specific ecological requirements, the dispersal capacity of these amphibians is likely limited which could conditionate our results. As (Peterson et al., 2002) highlighted, the probability of range expansion is probably species-dependent. In any case, evidence also suggest that at least lowland species can easily expand towards higher elevations (Araujo et al., 2005; Ballesteros-Barrera et al., 2022; Li et al., 2013).

The other factor that explains the low vulnerability is the fact that the projected suitable areas for almost all species still had suitable remaining forest and shrubland vegetation. However, this assumption has some difficulties and probably should be revised in the near future. Tropical dry forests are among the most threatened ecosystems worldwide and deforestation rates are even higher than those observed in humid tropical forests (Tapia-Armijos et al., 2015; Ferrer-Paris et al., 2018; Gaspar Miles et al., 2006; Sánchez-Azofeifa & Portillo - Quintero, 2011). It is estimated that close to 60% of the original dry forests in the Neotropics have already vanished, and it is expected that human pressure on these ecosystems will continue to increase (Portillo-Quintero & Sánchez-Azofeifa, 2010).Therefore, considering that 82% of these amphibians depend on forests (Todd et al., 2009) urgent conservation strategies are needed to protect the remaining habitat for the survival of habitat N-SDF endemic amphibians and to build suitable green infrastructures. Furthermore, it is also necessary to remind that the level of low intensity disturbance and degradation due to overgrazing and logging is a generalized concern (Jara-Guerrero et al., 2019) which could additionally limit the potential of many amphibians to disperse to suitable habitats.

Obviously, The fact that the suitable areas increase does not necessarily mean that they will be able to colonize or adapt to these new areas, since this will depend on the individual species requirements. For example, fossorial species could be limited by the type of soils, arboreal species depend on vegetation cover and aquatic species depend strongly on the quality of the water(Calderon et al., 2019; Lescano et al., 2015; Neckel-Oliveira & Gascon, 2006; Székely et al., 2018). There is evidence that climate change could affect amphibians in other ways. For example, climate change may alter hydrological regimes, which in turn can trigger microscale changes in aquatic habitats essentials for the development of the first life stages, facilitate disease spread, or alter the behavioral and physiological mechanisms for thermoregulation (Kiesecker et al., 2001; Lawler et al., 2010).

An additional concern is that the colonization of new areas by the focal species of our study could imply the generation of competition for the resident species (Davis, 2003). Resident species could be stressed due to the establishment of new competitors (Norberg et al., 2012), due to the competitive advantage that amphibians from dry tropical forests would have since they are more tolerant to high temperatures and have ecological adaptations to live in extreme environments (Catenazzi et al., 2014; Székely, et al., 2018). These biotic conflicts can be aggravated in species with narrow ecological niches (Urban et al., 2012). In fact, there is evidence (in birds, mammals and butterflies) that the expansion of species to higher altitude could produce local extinctions and the drastic contraction of specialists ranges (Peterson et al., 2002). Higher altitude areas, such as neotropical montane and cloud forests are rich in specialists, more vulnerable not only to climate change but also to other stressors such as the arrival of new colonizers and land use change (Laurance et al., 2011; Menéndez-Guerrero et al., 2020; Wake & Vredenburg, 2008).

Additionally, the projected changes in distribution (increase in high suitability area, the projection of upper slope movements and the increase in richness patterns) may produce not only novel competitive interactions, but also rearrangements in amphibian community's composition to novel communities (Botkin et al., 2007). It is expected that, in many cases, part of the N-SDF and a great proportion of montane forest will show an increase in richness and a decrease in β diversity, which means that these ecosystems will go through a homogenization process caused by the increase in generalist species and the loss of specialists. On the other hand, lowland areas such as Dry Chaco - Chiquitano and the Catinga- Cerrado will go through a heterogenization process, with an increase in β diversity (Menéndez-Guerrero et al., 2020).

We detected four amphibians with high vulnerability to climate change, all of them located in the Mexico and Central America nucleus. For this species, a great surface of their present and project suitable areas are already deforested. Two of these, *Exerodonta xera* and *Craugastor rugulosus,* have also been reported as highly vulnerable and "Critically Endangered" for Ballesteros- Barrera et al. (2022) who assures that these species will lose more than 50% of their suitable habitat under RCPs 4.5 and 8.5. The Mexico and Central America and the Dry Chaco and Chiquitano nuclei are the N-SDF with the highest values of mean vulnerability species concentration. These nuclei have been recently included in the IUCN Red List of Ecosystems within the categories "Endangered" and "Critically Endangered", respectively (Ferrer-Paris et al., 2018), mostly due to the high deforestation rates they experienced, the loss of suitable habitat due to climate change, and the lack of protection (Ballesteros-Barrera et al., 2022; Ferrer-Paris et al., 2019; Portillo-Quintero & Sánchez-Azofeifa, 2010; Prieto-Torres et al., 2016; Trejo & Dirzo, 2000). Our results reinforce this dramatic view. This should guarantee an improved protection for these dry forests in the future. As for the amphibians distributed in other N-SDF nuclei, the fact that vulnerability values are low indicates that climate change is not their main stressor, but deforestation and degradation could be imminent threats, emphasizing the urgency for studies focused on the loss of their habitat due to land use changes.

Synthesizing more than half of the amphibian endemics of the N-SDF gained range, in both extension and altitude, under the two climate scenarios suggesting that they could have suitable habitat in the future to colonize, as long as their life-history traits allows it and the vegetation cover is maintained. The analysed changes in patterns of richness by remaining habitat show, in most of the cases, a gain in the number of species, which implies that species will go from being dispersed to being more concentrated in the future, probably increasing the competition.

The vulnerability of these amphibians was medium for the RCP8.5 scenario (high emissions) and low for RCP4.5 (low-medium emissions). The dry forest regions with the highest vulnerability to climate change were Dry Chaco, Chiquitano, and Mexico and Central America. Our research emphasizes the need for conservation strategies which are based not only on the current distribution of the species, but also on vulnerability to future climate assessments; such analysis determines which areas with necessary vegetation cover could facilitate connectivity between the current and future ranges of each species. Although our lack of information on mechanistic relationships between species and their environments might restrict the scope of our conclusions, and potential distribution models have certain limitations, they are currently one of the most useful tools for species conservation.

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CAPÍTULO IV

Priority areas for amphibian conservation in Ecuadorian Pacific region

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Abstract

The Ecuadorian Pacific region is a seasonally dry forest, an area that is distributed in western Ecuador and northwestern Peru are challenging ecosystems, harboring a diverse and endemic amphibian community, consisting of at least thirty species. The scarcity of biological information and the lack of attention that these dry forests have received, together with their increasing threats, make urgent their adequate inclusion in the network of protected areas. The present work focuses on identifying priority zones for amphibian conservation within these SDFs, based on the potential distribution of all amphibian species known to occur there. We generate a priority index unifying data regarding species richness, endemicity and conservation threat, ranking the whole Equatorial SDF area into high, medium or low priority for amphibian conservation; we further evaluate the current status of protection and land cover/ use for each priority level. Our results show that less of a quarter of the high and medium priority areas are currently lacking any form of protection, and that almost half of the high priority areas are located in heavily disturbed sites. The fact that important areas in both medium and high priority levels are still harboring natural vegetation emphasizes the opportunity for conservation if immediate actions are taken to expand the protected area network, focusing on more diverse and endemic communities and creating biological corridors.

Key words: Anurans, dry forest ecosystems, Ecuador, frogs, Peru, toads.

Introduction

One of the most threatened and fragile ecosystems in the Neotropics *seasonally dry forest* (hereafter SDFs) is Ecuadorian Pacific region biodiversity hotspot (Sierra et al. 2002). These Ecuadorian and Peruvian forests are home to highly diverse and endemic biota (Linares-Palomino et al. 2010, Linares-Palomino et al. 2011). Among the fauna of these ecosystems, a taxon that has received little scientific attention are the amphibians. The Neotropical SDFs, due to their severe climatic conditions, is one of the most challenging ecosystems for these animals, generating a highly adapted diversity, represented in many cases by species with narrow distributions. Currently, 30 amphibian species have been reported from the Ecuadorian Pacific region, belonging to 14 genera and eight families of anurans (Armijos-Ojeda et al. 2021). This lack of information is surprising since amphibians are well known by their high extinction risk and ability to act as bioindicators, factors that have fueled their use to drive conservation policies in other neotropical ecosystems (Xu et al. 2008, Andersen et al. 2023).

Latin America is one of the most diverse regions in the world regarding amphibians, but also one of the most critically threatened, with generalized reports of amphibian decline and extinction (Lips & Reaser, 1999). Despite the fact that the Neotropical SDFs are one of the hotspots of endemism worldwide, and degradation and loss have reached huge values, these habitats retaining less than 44% of their original cover (Portillo-Quintero et al. 2015, Rivas et al. 2021), our information on the performance of some biological groups is very low. It is expected that most endemics would be experiencing abrupt declines and extinctions. Since the habitat loss is followed by extinction after a time-lag (Brooks et al. 1999), the high rate of deforestation alone should stimulate concentrated conservation measures (Brooks et al 2002). In the case of the Ecuadorian Pacific region, conservation is especially complicated by the scarce information that is available on these ecosystems. Therefore, it is important to provide data that allows us to recommend management actions and establish priority zones for the conservation of amphibians in the SDFs of the coastal region of Ecuador and Peru, thus mitigating threats to biodiversity and specifically to amphibians.

Protected areas (hereafter PAs), covering approx. 16% of the earth's land surface (UNEP-WCMC & IUCN 2022), are one of the most common and efficient ways to ensure the long-term persistence of species, especially in amphibians (Watson et al. 2014, Gray et al. 2016, Pacifici et al. 2020, Halstead et al. 2022). As part of the international effort, both Ecuador and Peru are supposed to increase the extension of their PA network until 2030 (Ministerio del Ambiente del Perú 2014, Ministerio del Ambiente del Ecuador 2016). However, it is unclear how effective the existing PAs are at covering the distribution of amphibians in the dry forests of these two countries (Fajardo et al. 2023), and which additional sites would represent a priority to optimize conservation efforts for these taxa.

Here, we aim to contribute information regarding the biodiversity patterns of amphibians in these threatened SDFs, to support effective conservation strategies and management (Myers et al. 2000). Based on the potential spatial distribution of the known species, their endemicity and their threat challenges, we generate an index of priority areas. We then compared their representation in the

PA network and evaluate what is the state of land cover and use. This comparison allows the identification of conservation gaps and can be used to propose the areas that would result most beneficial for amphibian conservation if included in the PA network.

Materials and methods

Study area

The Ecuadorian Pacific region which are semi-deciduous and deciduous vegetation (forests, shrublands), cover an altitudinal range between 0 and 1631 m a.s.l., have a seasonal rainfall distribution, annual precipitation varying between 500 and 1500 mm, and average annual temperatures over 17°C, high and fairly stable throughout the year. The region is delimited by humid ecosystems that house amphibian communities of different origin and with different physiological and morphological traits, such as the transition zones to the Andes mountains (foothills) in the eastern region and the transition zones to the Chocó rainforest in the north. The study area (Fig. 1) covers 55153.42 km^2, of which 36.5% is in Ecuador and 63.5% in Peru; it consists of a narrow band (3-150 km wide) bordering the Pacific Ocean, extending from the Ecuadorian province of Esmeraldas in the north to the Peruvian department of Lambayeque in the southernmost tip (Armijos-Ojeda et al. 2021).

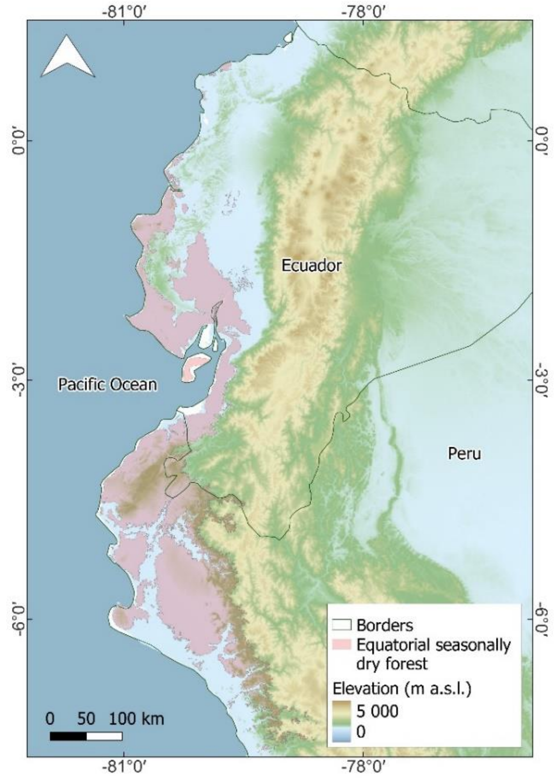

Figure 1. Location of the Ecuadorian Pacific region, based on Armijos-Ojeda et al. (2021).

Species distribution data

For the 30 amphibian species reported from the Ecuadorian Pacific region, we compiled a dataset of occurrence-only records, based on data points from Armijos-Ojeda et al. (2021). To update this dataset and complement occurrence data outside the SDFs to improve species distribution models, we added geo-referenced presence data from the following online repositories (latest date of search 2 February 2022): HerpNET (http://herpnet.org), Red Mundial de Información sobre Biodiversidad, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (http://www.conabio.gob.mx), Smithsonian National Museum of Natural History (https://naturalhistory.si.edu), Museum of Comparative Zoology, Harvard University (https://mcz.harvard.edu/), Museum of Vertebrate Zoology, University of California, Berkeley (http://mvz.berkeley.edu), Peabody Museum of Natural History (https://peabody.yale.edu/), Bioweb Ecuador (https://bioweb.bio), GBIF (http://www.gbif.org). Additionally, we carried out an electronic literature search (latest date of search on 1 February 2022) in the databases Web of Science, Google Scholar, and Scielo, using the terms <<species name>> AND “inventory” OR “distribution” OR “Belize” OR “Colombia” OR “Costa Rica” OR “Ecuador” OR “El Savador” OR “Guatemala” OR “Guyana” OR “Honduras” OR “Mexico” OR “Nicaragua” OR “Panama” OR “Peru” OR “USA” OR “Texas” OR “Venezuela”. To find older occurrence data, additionally to searches using currently accepted species names, we also used previous synonyms. Multiple records from the same location were removed. The dataset was taxonomically standardized and updated according to Frost (2022). Conservation status for the species was retrieved from IUCN (2022). We defined as endemic species that have their distribution range restricted to the Equatorial SDFs.

Environmental data

Based on the physiological requirements of amphibians, we selected 19 variables from Climatologies at high resolution for the earth's land surface areas - CHELSA (Karger et al., 2017) (https://chelsa-climate.org/). These variables have a spatial resolution of 30 arcseconds (~1 km).

Data preparation

We generated an analysis grid with a cell size of 1 km^2, reflecting the spatial resolution of the bioclimatic variables. Duplicate occurrence points in the same 1 km pixel were eliminated to avoid redundancies (Matias et al. 2024).

Species distribution models

Because amphibian surveys in the Ecuadorian Pacific region suffer from spatial biases, many areas being unsampled or inadequately explored (Armijos-Ojeda et al. 2021), we employed species distribution modelling to infer the patterns of amphibian distribution and assemblages they form, across the study area. We used MaxEnt software, version 3.4.4, to generate the potential habitat model for each of the 30 species analyzed. MaxEnt allows the creation of probability models based exclusively on presence data (Mahatara et al. 2021). The statistical significance of each model was evaluated by generating 5 replicates. The average of the 5 replicates was used to determine the optimal habitat suitability and performance of the models, which also helped to assess the uncertainty associated with the models (Ali et al. 2023).

Priority index

To delineate priority areas for amphibian conservation we employed three criteria: richness, endemicity, and conservation status. Each variable was standardized on a scale of 1 to 4, where 4 represents the highest priority. Species richness was obtained by converting the distribution maps of each species into binary predictions of presence and absence. These predictions were summed to generate a richness model (Grenié et al. 2020). The endemicity was calculated by counting the number of endemic species present in each pixel of the analysis grid (1 km²). In the case of the conservation status of the species, we assigned to each species a numerical value according to its conservation category, considering that different species could have different levels of threat. These values were summed for each pixel, which implies that species with different conservation categories can coexist in the same pixel. Subsequently, the three indicators were aggregated, and the resulting values were used to classify each pixel into high, medium or low priority for amphibian conservation (Table 1). All geospatial analyses were performed using QGIS software, version 3.14.0 (QGIS, 2022).

Table 1. Scoring model to determine priority levels for the Ecuadorian Pacific region, assigned according to the following criteria: number of amphibian species, number of species endemic to the Ecuadorian Pacific region, and their conservation status according to IUCN (2022). The scores for these criteria are summed to give the priority index for protection.

Score	Number of species	Number of endemics	Conservation status
1	0 – 4	0	NC / LC
2	5 – 9	1	DD
3	10 – 14	2	NT
4	15 – 19	3	VU

Afterwards, the various categories of priority were compared based on two variables: protection status and land cover and land use. For the official delimitation of PA, information was obtained from the Ministry of Environment, Water and Ecological Transition (MAATE) for Ecuador and from the National Service of Natural Areas Protected by the State (SERNANP) for Peru. The information for the two countries was standardized into the following categories:

- National: governmentally protected areas, created and funded by the state;

- Community: areas protected and managed by local communities, created but not funded by the state;

- Municipal: areas protected by municipalities (decentralized autonomous governments), created but not funded by the state;

- Private: declared, owned and funded by private entities, including NGOs;

- unprotected: areas that have no official protection status.

To determine land cover and land use, we used data provided by the Ministerio del Ambiente del Ecuador (2019) for Ecuador and by the Geo GPS Perú (2014) for Peru. The information was standardized into the following categories:

- Natural vegetation: areas covered by natural vegetation, such as forests, shrubs etc.;

- Crops and pastureland: areas used for agricultural and livestock production;

- Water bodies;

- Infrastructure: includes buildings, roads, bridges etc.;

- Other lands: areas devoid of vegetation, which due to their characteristics are not used for agricultural or forestry purposes.

This analysis gave us a more detailed understanding of the distribution of priority conservation areas in relation to the presence of PAs and the composition of the landscape in terms of land cover and land use in the study region.

Results

Based on richness, endemicity and conservation status of the amphibians, the 55079 km^2 of Equatorial SDFs were classified into low priority (91%), medium priority (7%) and only a tiny fraction of 2 % as high priority. Most of the low priority areas are in Peru, while medium and high levels have a higher proportion in Ecuador (Table 2). Both high and medium priority zones are concentrated towards the central coast and in the southwestern areas of Ecuador and northwestern

Peru (Fig. 2). In total, high and medium priority areas for the conservation of amphibians represented less than 5000 km^2.

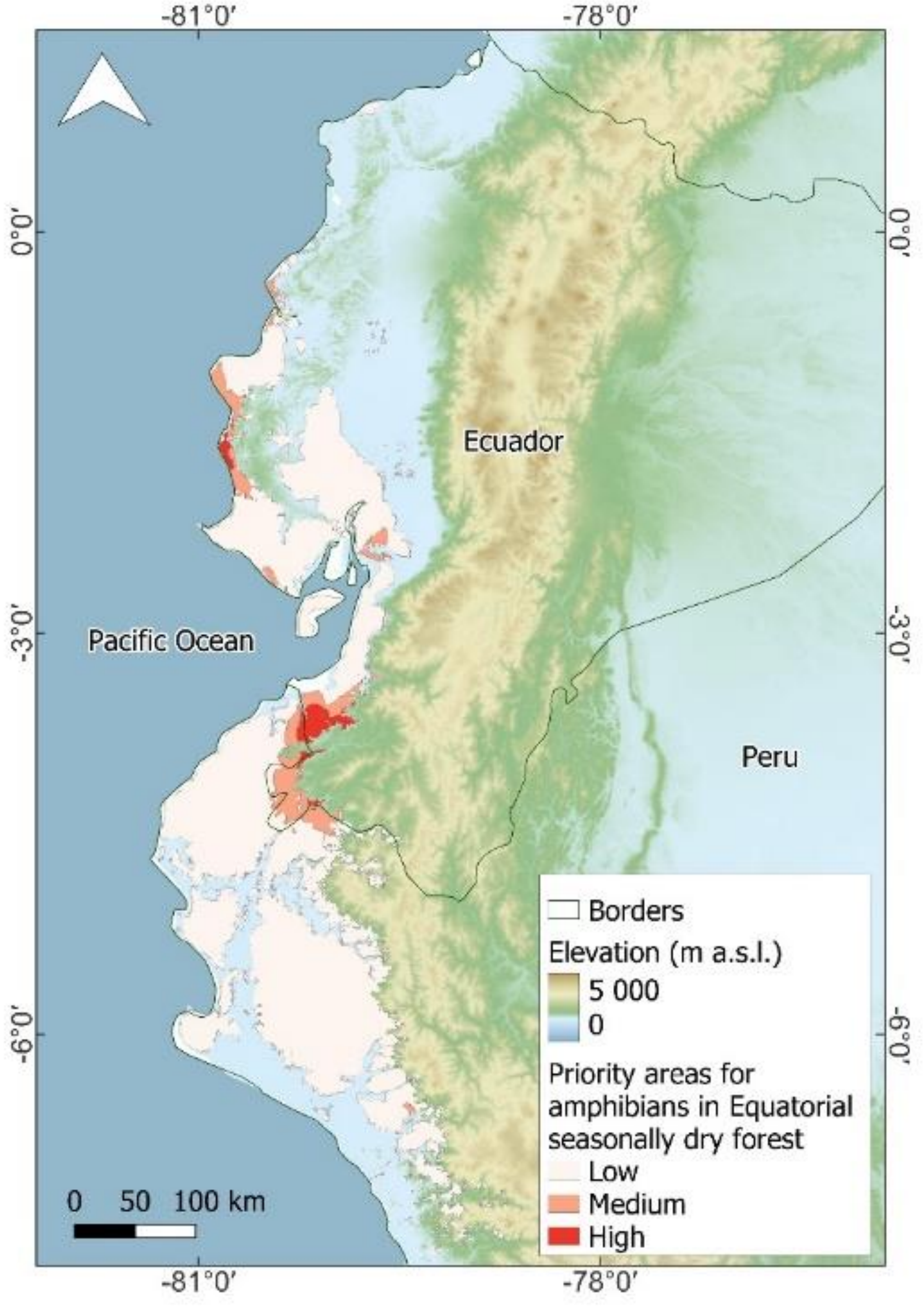

Figure 2. Distribution of priority areas for amphibian conservation in Ecuadorian Pacific region.

Table 2. Results of prioritization for amphibian conservation in the Equatorial seasonally dry forests. EC- Ecuador; PE – Peru. Protection type: Nat - governmentally protected areas, Priv - areas protected by private entities, Com: areas protected by local communities, Munic: areas protected by municipalities. Land cover/ use: N - natural vegetation, C - crops and pastureland, W - water bodies, I - infrastructure, O - other lands. Values are given in km^2 and percentages out of the corresponding priority category total area.

Priority level	**Total area**		**Protected area**	**Protection type**				**Land cover/ use**				
	EC	**PE**		**Nat**	**Com**	**Munic**	**Priv**	**N**	**C**	**W**	**I**	**O**
Low	50103		3570	2113	1286	37	144	37552	9070	925	795	1761
	15757	34346	7.1%	4.2%	2.6%	0.1%	0.3%	75%	18%	1.8%	1.6%	3.5%
Medium	3875		841	448	142	12	139	2555	1002	86	68	164
	2865	1010	21.7%	11.6%	3.7%	0.3%	3.6%	65.9%	25.9%	2.2%	1.8%	4.2%
High	1102		243	237	1	0	6	502	537	17	10	36
	859	242	22.1%	21.5%	0.1%		0.5%	45.6%	48.7%	1.5%	0.9%	3.3%

Regarding current protection status, only a 22.1% of the areas categorized as high priority are included in current PAs (national, community, municipal or private reserves); for the medium priority, only a 21.7% of the area is protected, and for the low priority, just 7.1% is included in any PA (Table 2). National PA have a larger extension among the Equatorial SDFs compared to other types of protection, both in Ecuador (National System of Protected Areas - SNAP) and Peru (National System of Natural Areas Protected by the State - SINANPE).

Regarding current land use, half of the high priority areas are situated in very transformed anthropic habitat, most of it in agricultural lands. The natural vegetation is maintained only in a 46% of the high priority and in 66% of the medium priority areas (Table 2).

Discussion

Current conservation of amphibians in the PAs of the SDFs in the region is extremely poor. The conservation of amphibians in these extremely threatened forests ecosystems is far from being guaranteed. Furthermore, our study reveals clear opportunities for amphibian conservation in these ecosystems, and can serve as input for the development of national and regional strategies for biological diversity through targeted expansion of the *in-situ* conservation network. In general, this under representation of amphibians in the network of PAs is increasing their extinction risk and prevents adequate mitigation measures for habitat degradation and fragmentation, climate change and invasive species (Nori et al. 2015). We found that less than a quarter of both high and medium priority areas are under some form of spatial protection, resulting in significant gaps in the safeguard of this endemic fauna and emphasizing the urgency to focus the conservation efforts towards these areas. It is likely that such gaps will become larger in the future due to climate change and habitat loss and degradation (Brooks et al. 2002). Even in the case of high priority areas which are located inside PAs, constituting a refuge for biodiversity, their small extension and isolation from similar well-preserved habitats converts them in islands vulnerable to extinction processes (Espinosa et al. 2016, Pabijan et al. 2020).

Along with the high priority areas, it is important to pay attention to the areas that were included in the medium priority category. The SDFs face many anthropogenic pressures that produce an accelerated change in land use, which may lead to a gradual loss of amphibian diversity (Suazo-Ortuño et al. 2018, Thompson & Donnelly 2018). In addition, the impacts that climate change may have on these species are still unknown, which may further aggravate the situation (Medina et al. 2020, Ballesteros-Barrera et al. 2022). This makes it all the more important to protect and guarantee preservation of the remaining areas in order to ensure areas of connectivity.

Most of the high and medium priority areas for amphibian conservation are concentrated towards the coast of Ecuador, despite the larger extension of these SDFs in Peru. This is due to the fact that our richness and endemicity models showed a lower concentration of amphibian species in Peru, towards the extremely arid Sechura desert. Both countries are making efforts to increase their PA extent (Van der Hoek 2017) and to guarantee the connectivity of dry forest remnants, including through the transboundary Biosphere Reserve “Bosques de Paz” which integrates the national PAs of northwestern Peru with private reserves, municipal reserves and PAs from southwestern Ecuador (UNESCO 2017, Iñiguez-Gallardo et al 2021).

Although our analysis separates between types of reserves based on their ownership, it does not take into account the differences in the level of restriction of human activity among the existing PAs. Generally, inclusion in a governmentally PA such as a national park/ reserve should offer the highest protection against anthropogenetic changes, especially land conversion and degradation; however, their efficiency differs, and some human interventions may be tolerated or permitted, which could be affecting the conservation of these amphibians (Van der Hoek 2017). Illegal deforestation is more intense in smaller PA, closer to agricultural lands and mining concessions, and in proximity to roads (Kleemann et al. 2022). On the other hand, PAs that are managed by local governments and local communities, due to their small size, are more vulnerable to border effects, pollution, although they are more likely to benefit from citizen support (Gravez et al. 2013). However, in accomplishing their conservation targets, they have been shown to perform worse than both national and private reserves, due to lower financial resources (López-Rodríguez & Rosado 2017).

An alternative to the public protection is represented by the privately owned reserves. In this case, the areas do not receive financial support from the state, but their designation as PAs through governmental decrees provides legal support. Depending on the funding from donors and with the support of local NGOs, such PAs promote the control of human interventions, conduct habitat restoration, research and community development. The efficiency of such efforts has been shown in many cases, some of them located in the Ecuadorian Pacific region, in spite of huge pressures from illegal logging, agricultural expansion and mining companies (Horstman 2017, López-Rodríguez & Rosado 2017). Despite their small size, the contribution of private reserves to strengthening the protected area network is critical because of effective planning and more agile and flexible management (Ivanova & Cook 2020).

In terms of land use, the areas categorized as medium priority have a high proportion (66%) of natural cover, which can be used for adequate management of the areas in this category, so that they could function as buffer zones for the high priority areas. The areas categorized as high priority have only 46% of natural vegetation, which makes conservation efforts urgent in these critical areas. However, even natural habitats in their SDFs have experienced significant structural changes as a result of human activities (Rivas et al. 2020, 2021), so that targeted conservation measures for amphibian species might be needed to meet conservation goals (Suazo-Ortuño et al. 2011, Lescano et al 2015).

The fact that a large proportion of the high-priority amphibian areas is located in agricultural lands show that the geographic ranges of most amphibians inhabiting the SDF overlap with heavily human-modified landscapes. The opportunities to conserve these amphibians in highly disturbed regions are poor, so the focus should be to urgently expand the network of protected areas by establishing biological corridors to link dry forest remnants.

In any case, robust and appropriate management regimes in the existent PAs or even in unprotected areas are a critical demand beyond the extension of formally protected areas for biodiversity conservation (Gray et al. 2016). Stricter regulations of human interventions are known to increase performance in terms of desire outcomes for biodiversity, but similar results can be accomplished through positive involvement of local communities. For example, by offering economic incentives to individual landowners or communities who agree to conserve valuable ecosystems has positive results not only for biodiversity but also through poverty alleviation (de Koning et al. 2011), the main drawback being finding sustainable sources of funding. Other measures, such as improved information on the purpose of management of established protected areas, increasing public awareness of biodiversity heritage and value, conservation strategies and fostering citizens participation in conservation actions, reduce human impact and result in systematic and efficient long-term gains for biodiversity conservation (Waylen et al. 2010, Haywood et al. 2016, Tran et al. 2020). All these measures, along with an ecologically representative protected area network, are our best hope in preserving the Ecuadorian Pacific region and their unique biodiversity.

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DISCUSIÓN GENERAL

Esfuerzo de muestreo de anfibios en los bosques secos

El trabajo desarrollado como parte de este trabajo doctoral permitió sistematizar y organizar una base de datos con más de 40.000 registros. Estos datos fueron obtenidos unificando toda la información disponible en la literatura científica y técnica, en bases de datos especializadas y con todos los registros de campo obtenidos durante más de 20 años por nuestro grupo de trabajo en la región Pacífico Ecuatorial y por otros expertos que han trabajado en diferentes áreas del Neotrópico. El esfuerzo desarrollado hasta la fecha para conocer la biodiversidad de anfibios en esta región ha sido una contribución significativa para generar una línea de base de referencia sobre la diversidad de anfibios en estos bosques, sin embargo, es altamente posible que estemos subestimando la diversidad real de anfibios, pues en los últimos años se han descrito nuevas especies para estos ecosistemas (Ron et al. 2010, 2018, Menéndez-Guerrero et al. 2024). Nuestra base de datos revela la existencia de vacíos de información espaciales muy importantes, al sur de América Central, en las Antillas menores, en la parte más continental de los bosques secos del Caribe (Colombia y Venezuela), al sur de la Caatinga – El Cerrado, costa norte de Perú, bosques secos interandinos (Perú y Bolivia), sur de la costa de Perú y desierto de Atacama (Cap. I y II). Esto sugiere que es posible que parte de la diversidad de estos ecosistemas aún no haya sido descrita.

Diversidad de anfibios en los bosques secos del Neotrópico

Los Bosques Neotropicales estacionalmente secos (BNES) se han convertido en un punto focal de investigación en la última década debido por un lado a sus elevados niveles de endemicidad y diversidad, y por otro por la enorme dependencia de sus servicios ecosistémicos y, sobre todo, por la fuerte tasa de degradación y destrucción a la que están sometidos (Rivas et al. 2020, Jara-Guerrero et al. 2021, Prieto-Torres et al. 2021).

En nuestro estudio encontramos que existe una gran diversidad de anfibios, pese a las condiciones ambientales extremas que caracterizan a los BNES, alcanzando 260 especies representadas en distintas familias con hábitos variados, de estas, 135 especies (51%) son endémicas de estos ecosistemas (Cap. I). En términos de riqueza, las regiónes más diversas corresponden a los bosques secos de México – Centroamérica (82 especies) y al Chaco Seco (59 especies,), ambas regiones hacia los extremos norte y sur del bosque seco Neotropical. A su vez, las regiones con menor riqueza son los valles secos interandinos de Boliva y Perú (6 especies) y las Antillas (21 especies).

Además, un factor importante que influye en la riqueza de los anfibios fue también la extensión de la región, siendo el Chaco seco (59 especies), la Caatinga – El Cerrado (49 especies) y los bosques etacionalmente secos de Mexico – Centroamérica (82 especies) los más grandes en superficie y los más diversos. Aparentemente, un área más grande ofrece una mayor diversidad de nichos ecológicos, además al estar rodeado de ecosistemas ricos en especies ha favorecido las oportunidades de colonización de estas comunidades hacia los bosques secos. Por el otro lado, las regiones más pequeñas de los BNES también mostraron niveles sorprendentemente altos de endemismo a pesar de su baja riqueza, por ejemplo, los bosques interandinos de Bolivia y Perú que tienen solo 6 especies de las cuales el 50% son endémicas, las Antillas que tienen 21 especies con un endemismo del 57% y los valles secos interandinos de Colombia que tiene 51 especies con un endemismo del 63%.

Las condiciones climáticas tuvieron una influencia significativa en la composición de las comunidades de anfibios. Por ello, lo que encontramos fue que tanto la disponibilidad de agua (representada por la cantidad de precipitaciones), como la cantidad de energía (temperatura media anual), y la heterogeneidad de estos dos parámetros a lo largo del año, fueron predictores significativos, con una influencia positiva en la riqueza de anfibios para las subregiones del BNES.

Hemos dedicado un esfuerzo especial al bosque seco de la región Pacífico Ecuatorial, porque es un ecosistema que llevamos explorando desde hace más de 20 años. Allí hemos identificado la presencia de 30 especies de anfibios, de las cuales más del 20% son endémicas de esta región (Cap. II). Todo el ensamblaje de especies de la región exhibe una diversidad de rasgos funcionales enorme incluyendo aspectos como el hábitat que usan, las estrategias reproductivas, el tipo de desarrollo y el tamaño corporal. Para la región hemos identificado también varios sesgos/deficiencias de los muestreos llevados a cabo, tanto políticos (muestreo mucho más pobre en el Perú pese a que la extensión de la región es mayor allí), como de preferencia (muestreos con predilección en áreas protegidas) y de logística (debido al difícil acceso en áreas remotas). En este sentido es importante enfatizar la necesidad de mantener los escasos esfuerzos de prospección de esta diversidad y en la medida de lo posible, promover esfuerzos nacionales e internacionales para conservar y conocer esta riqueza biológica.

Una importante característica de la diversidad de anfibios en los BNES es el grado de endemismo, cada región a lo largo del Neotrópico, presenta un conjunto de anfibios únicos que podría indicar una historia evolutiva independiente. Las diferentes regiones tienen en promedio un endemismo del 39%, destacándose los valles interandinos de Colombia (62% de endemismo) y las Antillas (57% de endemismo). Estos valores son extremadamente altos, para tener una idea de su importancia podemos comparar por ejemplo con el Ecuador, el tercer país más diverso de anfibios en el mundo, que tiene un endemismo de 47% de las especies, pero su riqueza incluye la diversidad de los más de 90 ecosistemas que posee este país (Ron et al. 2024).

A nivel de subregiones de bosque seco Neotropical, los patrones de diversidad de anfibios están caracterizados también por un alto endemismo (24% en promedio) y una elevada tasa de recambio entre ellas, lo que resalta la singularidad de cada una de estas áreas. La distancia espacial entre subregiones tuvo un efecto importante en la proporción de especies compartidas por las subregiones; de hecho, la separación generada por hábitats húmedos interpuestos entre ellas tuvo un efecto similar al de la insularidad. Este resultado parece estar relacionado con la baja capacidad de dispersión de los anfibios (Smith y Green 2005) y por el grado alto de adaptación de las especies en ecosistemas secos (Tracy y Christian 2005). Por ejemplo, los bosques estacionalmente secos de Perú (Sechura, Marañón), tienen una diversidad relativamente baja, pero con una proporción alta de especies únicas (55% de endémicas), rebasada por el bosque estacionalmente seco de la isla La Española (83% de endémicas), donde la insularidad marcada por el Caribe es muy evidente.

Vulnerabilidad de la comunidad de anfibios

A pesar de la importante riqueza y endemismo que muestran los BNES, cerca del 60% de su cobertura natural ya ha desaparecido, y se espera que la presión humana sobre estos ecosistemas siga aumentando (Portillo-Quintero & Sánchez-Azofeifa, 2010, Ferrer-Paris et al. 2019). Además, la proyección a futuro es que estos núcleos fragmentados serán desproporcionalmente afectados por el cambio climático, con efectos muy negativos sobre su biodiversidad asociados a cambios en la estructura de las comunidades, fisiología de las especies y cambios en las áreas de distribución (Prieto-Torres et al. 2020, Gonçalves et al. 2021, Ballesteros-Barrera et al. 2022). En este contexto, se determinó la vulnerabilidad al cambio climático de las especies de anfibios presentes en los BNES (Cap. III). Según nuestro análisis, las perspectivas de los anfibios que habitan los BNES pueden parecer optimistas, la mayoría de las especies están clasificadas en categorías bajas de amenaza por la UICN (Cap. I). De igual forma, los anfibios endémicos, la mayoría presentan una vulnerabilidad media o baja al cambio climático, y se prevé que más de la mitad de las especies mantendrán o incluso podrían incrementar su distribución en los escenarios futuros (Cap. III). Los modelos realizados, muestran que existirán cambios a futuro en los patrones de riqueza, mostrando un paranorama donde para la mayoría de los casos, las especies deberán enfrentarse a nuevos retos ambientales. Por ejemplo, los cambios en los patrones de riqueza proyectados, incrementarán la competencia interespecífica y en algunos casos implicarán una homogenización de las comunidades de anfibios a escalas espaciales grandes, debido a un aumento de las especies generalistas y una pérdida acentuada de las especialistas (Menéndez-Guerrero et al. 2020). En el caso de la posibilidad que tienen las especies para migrar desde zonas donde actualmente hay bosque seco hacia áreas de mayor altitud, la adaptación dependerá de los requerimientos específicos de cada especie (tipo de suelo, calidad de agua o tipo de vegetación (Székely et al. 2018, Lee et al. 2022) así como los síndromes de dispersión de cada una de estas especies.

Nuestro análisis de la vulnerabilidad al cambio climático no tiene en cuenta aspectos relacionados a fragmentación e integridad ecológica, que pueden limitar la conectividad en los próximos años. Esto es importante considerar, ya que podría impedir que, en el futuro, los anfibios puedan trasladarse a nuevos hábitats con condiciones favorables, y más aun, viendo las tasas de deforestación y disturbio crónico de estos bosques. De hecho, el caso particular la región Pacífico Ecuatorial nos indica que una gran proporción de las áreas de alta prioridad para la conservación de los anfibios ya está ubicada en paisajes fuertemente modificados, en especial en tierras agrícolas de las que difícilmente podrán escapar (Cap. IV). Las oportunidades para conservar estos anfibios en regiones altamente perturbadas son escasas, por lo que la atención debería centrarse en ampliar urgentemente los sistemas de áreas protegidas, mediante el establecimiento de corredores biológicos que unan los remanentes de bosque seco con los posibles refugios futuros.

Un aspecto especialmente preocupante es que los BNES más diversos en términos de anfibios (los núcleos de México – Centroamérica y el Chaco seco, Cap. I) son también las regiones que mostraron la mayor vulnerabilidad frente al cambio climático (Cap. III). Detectamos cuatro especies de anfibios con alta vulnerabilidad al cambio climático, todos ellos ubicados en el núcleo de México – Centroamérica. Para estas especies, una gran superficie de las áreas favorables actuales y futuras ya se encuentran deforestadas, poniendo en peligro su supervivencia en un futuro cercano (Ballesteros-Barrera et al. 2022). En cuanto a los anfibios distribuidos en otros núcleos del BNES, el hecho de que los valores de vulnerabilidad sean bajos indica que el cambio climático no es su principal factor de estrés, pero la deforestación y degradación de los bosques podrían ser amenazas inminentes, o podrían encrementar su intensidad en muy poco tiempo, enfatizando la urgencia de estudios centrados en la pérdida de su hábitat por cambios de uso de suelo (Ceballos & García 1995, Portillo-Quintero et al. 2015, Banda et al. 2016).

Aunque como hemos indicado la destrucción de bosques es la norma en la mayor parte del Neotrópico seco, existe evidencia que la región Pacífico Ecuatorial está sometida a una fuerte presión antrópica, experimentando una dramática pérdida de superficie y calidad de estos bosques, haciendo que la necesidad de conservación sea urgente (Jara-Guerrero et al. 2019). Nuestros resultados indican que las áreas de máxima prioridad en la región Pacífico Ecuatorial representan una ínfima fracción de la extensión evaluada (2%), y más de la mitad de estas son representadas por terrenos con alta intervención humana donde el futuro parece dibujar ua desaparición rápida. Incluso los hábitats naturales han experimentado cambios estructurales significativos como resultado de las actividades humanas (Rivas et al. 2020, 2021), por lo que podrían ser necesarias medidas de conservación específicas para cada especie de anfibio en un futuro próximo (Suazo-Ortuño et al. 2011, Lescano et al. 2015).

Por el otro lado, en la región Pacífico Ecuatorial, menos de una cuarta parte de las zonas de prioridad alta y media están incluidas en alguna forma de protección, lo que resulta en la existencia de importantes vacios para la conservación de esta fauna endémica. Nuestros resultados resaltan la urgencia de revisar y reforzar los esfuerzos de conservación que se están llevando a cabo en la región (Cap. IV). Incluso en el caso de áreas de alta prioridad que se encuentran dentro de áreas protegidas, su pequeña extensión y aislamiento de hábitats similares bien conservados, las convierte en islas extremadamente vulnerables a la degradación que puede disparar los procesos de extinción local (Espinosa et al. 2016, Pabijan et al. 2020). Todo ello enfatiza la necesidad de que las especies con distribución restringida sean objeto de medidas urgentes de monitoreo y conservación (Sodhi et al. 2008).

Nuestro estudio revela oportunidades claras para la conservación de anfibios en estos ecosistemas y puede servir como insumo para el desarrollo de estrategias, nacionales y regionales, que ayuden a la conservación de la diversidad biológica de anfibios a través de mejorar los esfuerzos de conservación *in situ*. Esta propuesta se puede extender a otras regiones y ser actualizada cuando la información complementaria esté disponible. Por ejemplo, la inclusión de rasgos funcionales (que actualmente se desconoce para muchas de las especies) podría ofrecer una imagen más completa de las comunidades de anfibios nativos y su capacidad para resistir a los cambios del paisaje, así como las diferencias de nicho entre ellas lo cual puede hacer su gestión para la conservación más eficaz y específica.

Se recomienda que la priorización de medidas de conservación considere en el futuro la diversidad funcional en conjunto y no solo la riqueza de especies, ya que todas cumplen un rol diferenciado en el funcionamiento del ecosistema (Campos et al. 2017, Bolochio et al. 2020, Button & Borzée 2021). Un análisis que incluya el modelamiento de la cubertura vegetal y/o uso de suelo en los escenarios futuros podría facilitar la conectividad entre la distribución actual y futura de cada especie. El conocimiento insuficiente sobre las amenazas y riesgos de las especies de anfibios que viven en los bosques estacionalmente secos del Neotrópico, además del hecho de que algunas han sido descritas recientemente, tiene como resultado un futuro incierto para las comunidades de anfibios que se han adaptado a la vida en esto ambientes áridos.

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CONCLUSIONES

Con la realización del trabajo doctoral, se la llegado a las siguientes conclusiones:

- A pesar de las limitaciones ecológicas que representan los bosques secos Neotropicales, albergan una importante riqueza de anfibios (260 especies), con un 51% de especies endemicas (135 especies). Existen subregiones como los bosques secos de Centroamérica donde el endemismo puede llegar al 82% de las especies. Además, se estudió a detalle la región Pacífico Ecuatorial, que incluye 30 especies de anfibios de las cuáles la tercera parte, son endémicas del ecosistema. En los bosques secos Neotropicales, se han identificado zonas con vacíos de información lo que podría estar generando una subvaloración de la riqueza total de estos ecosistemas.
- La diversidad de anfibios de las diferentes regiones de bosque seco Neotropical está determinada principalmente por la disponibilidad de agua y temperatura, que fueron predictores importantes de la riqueza. Además, la conectividad y el tamaño de las subregiones influyen positivamente en el número de especies presentes en cada una de las subregiones estudiadas. El área de las regiones influye en la riqueza específica, pero no está relacionada con el porcentaje de endemismo. En lo que corresponde a la región Pacífico Ecuatorial, la mayor riqueza se concentró hacia el centro y norte de la región, la baja riqueza hacia el sur está asociada a las condiciones climáticas que determina la cercanía al desierto de Sechura.
- El cambio climático es una amenaza potencial para los anfibios presentes en los bosques secos Neotropicales. Si bien, la mayoría de especies muestran una vulnerabilidad media o baja ya que ampliarían su área de distribución geográfica, hay que considerar que el potencial de estas especies para colonizar nuevas áreas es complejo, ya que depende de la disponibilidad de hábitats adecuados, la competencia interespecífica y su capacidad de dispersión. Por ello, las estrategias de conservación no deben centrarse solo en las distribuciones actuales y futuras, sino que deben considerar temas como la calidad del hábitat remanente y la historia natural de las especies, que puede incluir una variedad de rasgos funcionales, tal como lo hemos observado para la región Pacífico Ecuatorial.

- Los esfuerzos actuales de conservación de anfibios en la región Pacífico Ecuatorial son insuficientes y existen vacios importantes en lo que se refiere a la efectividad de las áreas protegidas para conservar la diversidad de este importante grupo. Las estrategias de conservación deberían centrarse en ampliar los sistemas de áreas protegidas y garantizar la conectividad entre los remanentes de bosques, considerando tanto las reservas gubernamentales como las privadas y comunitarias, que desempeñan un papel fundamental en estos esfuerzos.

Epipedobates anthony
Rana nodriza

Noemi Cevallos ©Picturatus