Herpetological Conservation and Biology 21(1):1–14.
Submitted: 2 May 2025; Accepted: 24 November 2025; Published: 30 April 2026.

Research Trends and Information Gaps in Amphibian Research in Costa Rica: Implications for Conservation

***Carolina Esquivel*[1,3], *Jessica Gómez-Orozco*[1], *Daniela Salazar-Sánchez*[2], *and Steve A. Stephens-Cárdenas*[2]**

[1]*Laboratorio de Biología Tropical, Escuela de Ciencias Biológicas, Universidad Nacional, Avenida 1 Calle 9, Heredia, 40101, Costa Rica*
[2]*Escuela de Ciencias Biológicas, Universidad Latina de Costa Rica, 100 metros norte y 25 metros este de Muñoz y Nanne, San Pedro, San José, 11501, Costa Rica*
[3]*Corresponding author, e-mail: caroesquiveldobles@gmail.com*

***Abstract*.—Amphibians are key components of ecosystems yet remain underrepresented in research compared to other vertebrates. With 41% of amphibian species globally threatened, addressing knowledge gaps is critical. Costa Rica harbors 222 amphibian species, of which 37% are classified by the International Union for Conservation of Nature (IUCN) as Vulnerable, Endangered, Critically Endangered, or Data Deficient. We conducted a systematic review of peer-reviewed literature on Costa Rican amphibians published between 2000 and 2022, compiling 327 studies and analyzing taxonomic, thematic, spatial, and collaborative patterns. Research was strongly biased toward frogs (Anura), while salamanders (Caudata) and caecilians (Gymnophiona) were scarcely studied. Most species reported belonged to common or abundant taxa, with 28 species lacking publications altogether. Ecological and behavioral studies predominated, whereas genetics, evolution, and biochemistry were rarely addressed. Geographically, research concentrated in accessible areas, covering only 1.35% of the territory of Costa Rica, with no records from Paramo ecosystems. Nearly 58% of sampled sites were outside protected areas, and only 47 of 147 terrestrial protected areas had amphibian research. Collaborations involved 236 institutions from 33 countries, with the U.S. and Germany the leading partners. Despite an increase in publications in recent years, threatened and Data Deficient species, high-montane ecosystems, and invasive taxa remain largely overlooked. Addressing these gaps will require innovative methods such as environmental DNA, strengthening local–international partnerships, and prioritizing underrepresented taxa and habitats. Our synthesis highlights both advances and persistent biases in amphibian research in Costa Rica, offering guidance for future conservation and management strategies.**

Key Words.—herpetofauna, systematic review, research bias, Anura, Caudata, Gymnophiona.

Introduction

Amphibians play major functional roles in ecosystems, maintaining biological diversity and facilitating ecological processes as both predators and prey (Amaral et al. 2019; López-Bedoya et al. 2024). The volume of scientific publications focusing on amphibians, however, remains disproportionately low when compared to other vertebrate groups (Christoffel and Lepczyk 2012; Meiri and Chapple 2016). Among terrestrial vertebrates, amphibians are one of the most diverse taxonomic groups, with over 8,900 recognized species (AmphibiaWeb https://amphibiaweb.org. [Accessed 30 October 2025]), and also one of the most threatened, with 41% classified as imperiled (International Union for Conservation of Nature [IUCN] 2021). This group has experienced population declines since the 1980s, raising concern within the scientific community (Amaral et al. 2019; Roll et al. 2017; Winter et al. 2016).

Human activities pose a significant threat to the survival of many amphibian species, through habitat loss and degradation, the introduction of exotic species, overexploitation, illegal trade, the spread of emerging infectious diseases such as chytridiomycosis and ranavirus, and the impacts of global climate change (Gibbons et al. 2000; Urbina-Cardona and Flores-Villela 2010; Luedtke et al. 2023). As a result, many amphibian species are undergoing destabilization of their ecological dynamics, which can lead to changes in population growth rates, loss of genetic diversity, fluctuations in population size, alterations in behavioral and reproductive patterns, home range displacement, and shifts in microhabitat use (Urbina-Cardona 2008). Most of these changes have resulted in local or global extinction events (Di Marco et al. 2018).

Costa Rica is a megadiverse country that harbors 222 amphibian species (J. Rodríguez et al. 2020), representing approximately 2.5% of the amphibian diversity of the world (AmphibiaWeb, https://amphibiaweb.org [accessed March 2026]). As of 2022, there are 222 known amphibian species in the country (157 Anura, 57 Caudata, eight Gymnophiona),

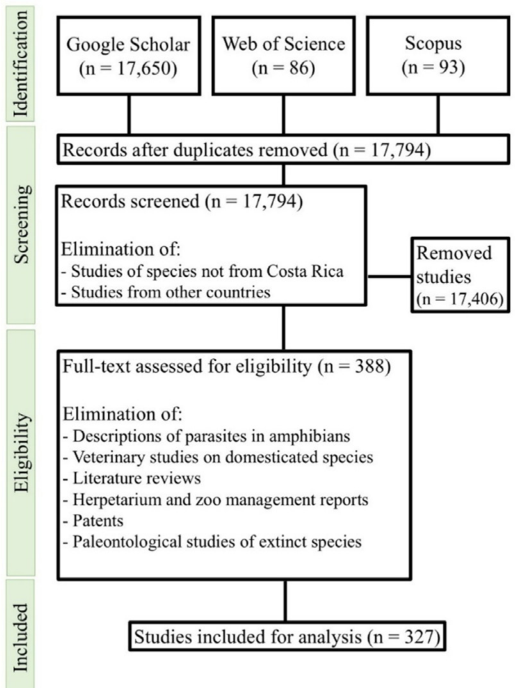

Figure 1. Selection process of relevant literature for amphibians of Costa Rica from 2000 to 2022.

of which 37% (n = 82 species) are categorized as threatened or Data Deficient according to criteria of the IUCN (J. Rodríguez et al. 2020). The country has a long tradition of conservation and herpetological research (Savage 2002). Nevertheless, despite the considerable amount of research being conducted on amphibians in Costa Rica, including peer-reviewed articles, theses, conference papers, and field guides, it remains unclear whether the limited resources available for this research are being allocated where they are most needed.

Previous studies have shown that systematic reviews of literature are powerful tools for compiling and analyzing results from various studies to address broad ecological questions (Scott et al. 1994; Winter et al. 2016). This study aims to identify taxonomic and spatial gaps in amphibian research over the last two decades through a systematic review of publications focused on amphibians, either conducted in Costa Rica or involving species collected from the country. Our objectives were to characterize: (1) geographic and taxonomic patterns of amphibian research in Costa Rica; (2) publication trends and coverage of research topics; and (3) target geographic areas, topics, and taxonomic groups that should be emphasized in future research. This represents the first attempt to compile research studies on Costa Rican amphibians over the last two decades, thus providing a key tool to guide prioritization and resource allocation for further investigation.

Materials and Methods

We conducted a systematic literature review to gather information on research about extant amphibian species in Costa Rica between January 2000 and December 2022. In each search, we combined the taxonomic keywords Anura, Caudata, and Gymnophiona with Costa Rica. Preliminary searches using broader or common-name terms (e.g., frog, salamander, *Rana*) yielded numerous irrelevant results, including studies from other regions and non-peer-reviewed documents. To maximize precision and ensure relevance, we restricted our search to the taxonomic names of the three amphibian orders.

Our analysis focused exclusively on peer-reviewed scientific articles. We excluded gray literature such as books, literature reviews, theses, herpetarium and zoo management reports, patents, and paleontological studies of extinct species. We also excluded veterinary studies on domesticated species and descriptions of parasites because these works were largely centered on the biology of the parasite or the pathology, providing limited information directly related to the biology, ecology, or conservation of amphibians as focal organisms.

We created the initial database using the public search engine Google Scholar (GS; Google, Mountain View, California, USA), which retrieves a diverse range of publications from both commercial and non-commercial publishers (Gehanno et al. 2013). We performed additional searches using the Web of Science (WoS; Clarivate, London, England, UK) and Scopus (Elsevier, Amsterdam, North Holland, Netherlands) databases to validate and refine our findings. The final database was curated to remove duplicates and documents not meeting the acceptance criteria above (Fig. 1).

From each selected publication, we extracted bibliometric data including year of publication, title, names of the authors, affiliations, language, length of the article (research paper or short communication), and the journal of publication. We thoroughly examined each document to identify the species included in the analysis. We reviewed scientific names and updated them when required, according to the Amphibian Species of the World database (Frost 2024). We obtained the conservation status of each species from a national IUCN Red List workshop report, which assessed most species with populations distributed within national boundaries (J. Rodríguez et al. 2020). Species not included in this report correspond to newly described taxa published after the workshop. We treated these as Not Evaluated (NE) because no conservation status had yet been assigned at either the national or global level.

Each publication was classified into one of 14 exclusive thematic categories, according to its primary subject: (1) Ecology (foraging and diet, ecological interactions, responses to abiotic conditions, phenology, population abundance and demographic parameters); (2) Geographic Distribution and Niche Models (geographic distributions, range extensions, niche models); (3) Phylogenetics and Systematics (diversification, phylogenetic assessment, taxonomy); (4) Evolution (population genetics, character evolution); (5) Phylogeography and Biogeography (spatial distribution of genetic variation, historical biogeographic patterns); (6) Descriptions (tadpole descriptions, body parts or coloration descriptions); (7) Diversity (species lists, diversity assessments); 8) Ontogeny (embryonic or juvenile development); (9) Biochemistry (biochemical compounds, toxicity, molecular ecology); (10) Diseases and Epidemiology (emergent and non-emergent diseases, skin microbiota); (11) Genetics (genome characterization, gene and genome sequencing, microsatellite development); (12) Behavior (bioacoustics and communication, reproductive behavior, locomotion); (13) Declines and Rediscoveries; and (14) New species (descriptions of new species). We defined these thematic categories *a priori*, based on major research areas commonly used in amphibian studies and bibliometric analyses. After compiling the database, we refined and finalized these categories *a posteriori* to ensure they adequately represented the diversity of topics found in the literature.

We obtained georeferenced coordinates for the sampling locations visited in each document. In cases where georeferenced locations were not available, we used the Google Earth search engine to assign a geospatial reference to the closest location name provided in the document. Although we included all studies published between 2000 and 2022 in the overall analyses regardless of sampling date, we restricted geographic analyses to locations sampled from 2000 onward. We also excluded duplicate locations, such as those reported in studies using the same samples. We performed spatial analysis of the sampling locations using QGIS 3.34 software (QGIS.org. 2024. QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.org). To estimate sampling frequency per unit area as a rough measure of geographical representativity, the total area of Costa Rica was divided into 1 km² grids.

We obtained national landscape and geopolitical variables (e.g., administrative boundaries, elevation), as well as the most recent base maps of protected areas (including national parks, national wildlife refuges, protected zones, biological reserves, absolute natural reserves, and wetlands), and the Holdridge Life Zones from the website of the Instituto Geográfico Nacional de Costa Rica (IGN), the public geographic authority of the country (www.snitcr.go.cr). We downloaded a digital elevation model (DEM) with a resolution of 30 arcseconds (1 km²) from the WorldClim 2.1 database (Fick and Hijmans 2017). We conducted subsequent qualitative and quantitative analyses using R version 4.4.2 (R Development Core Team 2024).

Additionally, we used correlational algorithms to generate bibliometric networks that allow identifying connectivity between institutions and countries (Perianes-Rodriguez et al. 2016) using the VOSViewer 1.6.18 software (van Eck and Waltman 2014). This analysis allowed us to get a broad understanding of how amphibian research has developed in Costa Rica. In these networks, the size of the nodes reflects the frequency of appearance in publications, while the width of the links is an indicator of the frequency of shared publications/collaborations.

Results and Discussion

We found 17,829 publications (GS = 17,650, WoS = 86, and Scopus = 93; Fig. 1). After removing duplicates and excluding studies of species from other countries, 388 papers remained. After evaluating eligibility criteria, we obtained a final database of 327 studies (Supplemental Information Table S1). Most of the papers addressed the biology of a single species (n = 208), while the remaining studies focused on two to a maximum of 68 species in a single paper, as in bioinventories. In total, there were 1,327 reports (term defined below), corresponding to 193 species. We use the term report to denote each instance in which a species was recorded in a publication. Thus, a single article mentioning five species would contribute five reports to our dataset.

Most publications were research papers (n = 245), and 82 were notes. The total number of publications per year ranged from four to 22, with a mean of 14 papers/y. The average number of papers/year in the

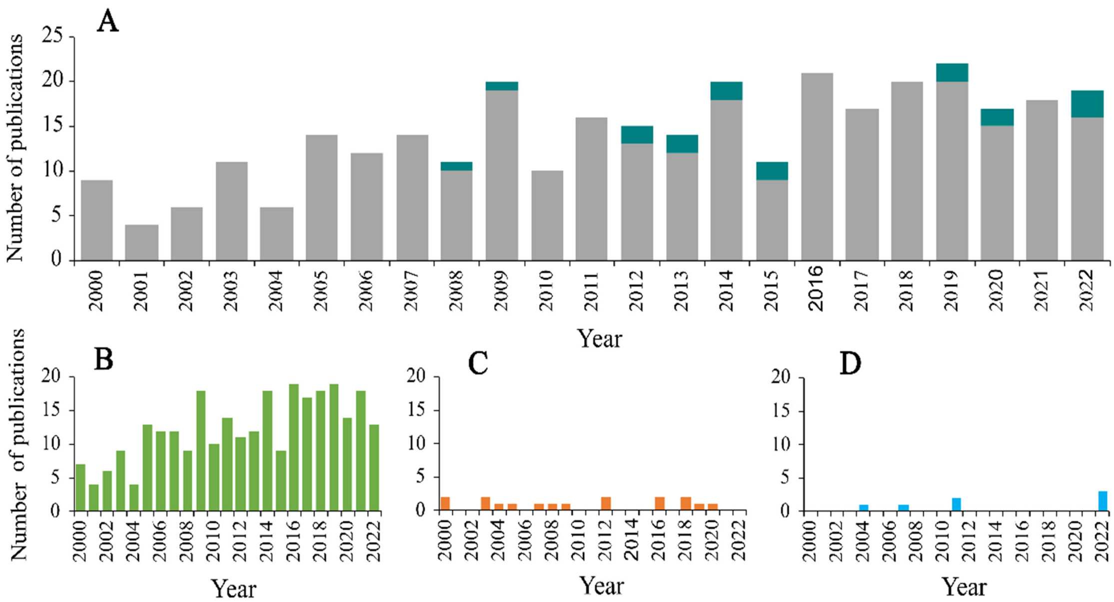

Figure 2. Number of publications per year for amphibian species of Costa Rica, from January 2000 to December 2022 (n = 327 total). (A) Number of publications per year for a single amphibian order (grey) and publications per year for a combination of amphibian orders (n = 17; teal). Number of publications per year for (B) Anura (n = 286), (C) Caudata (n = 17), and (D) Gymnophiona (n = 7).

first 11 y of our study was 11 ± (standard deviation) 4.5, while in the last 11 y, it increased to 18 ± 3.18 publications/y. This indicates that 66% of all papers (n = 215) were produced in the last 11 y of our study period (Fig. 2), reflecting a growing interest in amphibian research in Costa Rica.

Taxonomic patterns.—We found 286 papers covered anuran species, 17 covered salamander species, seven were about caecilians, and 17 publications included a combination of two or three orders (Fig. 2). Anuran species had the most prominent research interest with a publication frequency of 13 papers/y, while studies on Caudata and Gymnophiona were considerably scarce, with 0.7 and 0.3 papers/y, respectively. Gymnophiona had no publications from 2012 to 2021 and only appeared in diversity inventories. These disparities likely stem from differences in diversity, as anurans are four times more diverse than salamanders and 26 times more diverse than caecilians. Additionally, the difficulty in locating salamanders and caecilians, due to their secretive habitats and lack of vocalization, contributes to limited knowledge about these groups (Wake and Koo 2018).

Out of 222 amphibian species reported for Costa Rica, 193 appeared in at least one publication (Supplemental Information Table S2). The families with the largest number of papers were Hylidae (18.8%), Craugastoridae (15.5%), and Dendrobatidae (15.5%; Fig. 3). When considering species diversity, the families Plethodontidae, Hylidae, and Craugastoridae were the most represented. These are also the most speciose families in the country, with 58, 41, and 31 species, respectively.

The Strawberry Poison Frog (*Oophaga pumilio*) was the most studied species, with 66 published papers (Fig. 3), serving as a model organism in fields such as aposematism (Paluh et al. 2014; Willink et al. 2013), color evolution (A. Rodríguez et al. 2020), territoriality (Meuche et al. 2011; Staudt et al. 2010), and parental care (Stynoski 2009). The Striated Webfoot Salamander (*Bolitoglossa striatula*) was the most studied salamander species with seven papers published. Gymnophiona was represented by a strikingly low number of publications (Fig. 4), the majority focusing on the Purple Caecilian (*Gymnopis multiplicata*), a common and widespread species (Leenders 2017). The 10 most-studied species beyond *O. pumilio* were anurans characterized by abundance, tolerance to disturbance, and wide distribution. Forty-seven species accounted for 63% of reports (n = 836), while 146 species were infrequently studied, with 44 cited only once, often in diversity assessments. Importantly, 28 species lacked peer-reviewed studies during the study period (Table 1). The absence of publications on these taxa is likely related to their elusive habits (fossorial or canopy-

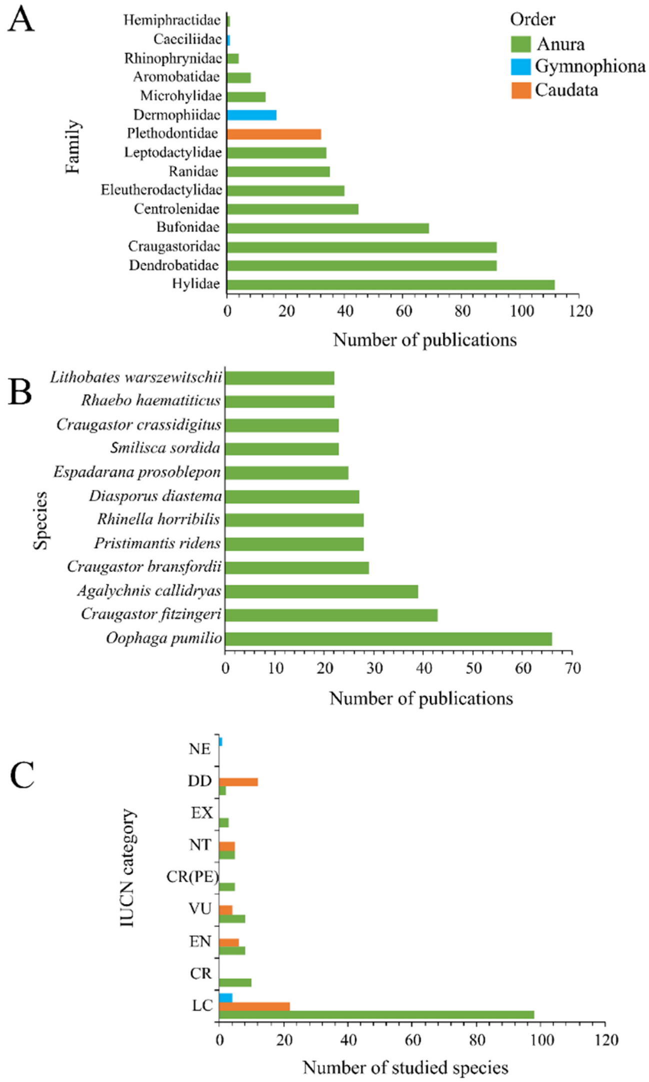

Figure 3. (A) Number of publications found for each of the amphibian families reported for Costa Rica. (B) Most studied amphibian species in Costa Rica, from top to bottom: Brilliant Forest Frog (*Lithobates warszewitschii*), Smooth-skinned Toad (*Rhaebo haematiticus*), Slim-fingered Rain Frog (*Craugastor crassidigitus*), Drab Streamside Tree Frog (*Smilisca sordida*), Emerald Glass Frog (*Espadarana prosoblepon*), Common Dink Frog (*Diasporus diastema*), Cane Toad (*Rhinella horribilis*), Pigmy Rain Frog (*Pristimantis ridens*), Bransford's Litter Frog (*Craugastor bransfordii*), Red-eyed Leaf Frog (*Agalychnis callidryas*), Common Rain Frog (*Craugastor fitzingeri*), Strawberry Poison Frog (*Oophaga pumilio*). (C) Number of studied species categorized by the International Union for Conservation of Nature (IUCN) conservation status. The IUCN Red List categories are: Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct (EX), Not Evaluated (NE), Critically Endangered possibly extinct CR(PE).

dwelling), unresolved taxonomic status, or the lack of known populations (J. Rodríguez et al. 2020).

Five invasive amphibians have been reported in Costa Rica: Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*; Savage 2002), Puerto Rican Coqui (*Eleutherodactylus coqui*; García-Rodríguez et al. 2010), Greenhouse Frog (*Eleutherodactylus planirostris*; Barquero and Araya 2016), American Bullfrog (*Aquarana catesbeiana*; J. Rodríguez et al. 2020), and the Cuban Tree Frog (*Osteopilus septentrionalis*; Savage 2002). Only *E. coqui* and *E. planirostris* were studied, highlighting a significant knowledge gap (Falaschi et al. 2020). Gathering information about invasive species becomes crucial for understanding their population status, ecological interactions, and potential threats to local fauna (Falaschi et al. 2020).

Table 1. Costa Rican amphibian species with no published research from 2000 to 2022. Red List Categories of The International Union for Conservation of Nature (IUCN) are: Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct (EX), Not Evaluated (NE). Header abbreviations are WKN = without known populations, TP = taxonomic problems, I = invasive species, KOH = known only by holotype.

Order	Family	Species	IUCN	Habits	WKN	TP	I	KOH
Anura	Centrolenidae	*Cochranella euknemos*	LC	Vegetation	x			
Anura	Craugastoridae	*Craugastor gulosus*	DD	Leaflitter	x			
Anura	Craugastoridae	*Pristimantis gaigei*	LC	Leaflitter	x			
Anura	Craugastoridae	*Pristimantis pardalis*	LC	Vegetation	x			
Anura	Craugastoridae	*Strabomantis bufoniformis*	LC	Stream	x			
Anura	Hylidae	*Isthmohyla debilis*	CR	Vegetation	x			
Anura	Microhylidae	*Ctenophryne aterrima*	LC	Fossorial	x			
Anura	Craugastoridae	*Pristimantis moro*	LC	Arboreal	x	x		
Anura	Hylidae	*Duellmanohyla lythrodes*	DD	Vegetation	x	x		
Anura	Craugastoridae	*Craugastor rayo*	DD	Stream		x		
Anura	Eleutherodactylidae	*Eleutherodactylus johnstonei*	LC	Vegetation			x	
Anura	Hylidae	*Osteopilus septentrionalis*	LC	Vegetation			x	
Anura	Ranidae	*Aquarana catesbeiana*	LC	Aquatic	x		x	
Anura	Craugastoridae	*Craugastor cuaquero*	DD	Vegetation				x
Anura	Craugastoridae	*Craugastor phasma*	DD	Stream				x
Anura	Hylidae	*Ecnomiohyla fimbrimembra*	VU	Canopy				
Caudata	Plethodontidae	*Bolitoglossa marmorea*	LC	Moss banks	x			
Caudata	Plethodontidae	*Bolitoglossa schizodactyla*	EN	Arboreal	x			
Caudata	Plethodontidae	*Nototriton major*	CR	Moss banks	x			
Caudata	Plethodontidae	*Oedipina alfaroi*	VU	Semifossorial	x			
Caudata	Plethodontidae	*Oedipina collaris*	DD	Semifossorial	x			
Caudata	Plethodontidae	*Oedipina grandis*	EN	Semifossorial	x			
Caudata	Plethodontidae	*Oedipina carablanca*	EN	Moss banks				
Caudata	Plethodontidae	*Oedipina cyclocauda*	LC	Semifossorial				
Gymnophiona	Dermophiidae	*Dermophis costaricense*	DD	Fossorial	x			
Gymnophiona	Dermophiidae	*Dermophis gracilior*	DD	Fossorial	x			
Gymnophiona	Caecilidae	*Oscaecilia osae*	DD	Fossorial	x			
Gymnophiona	Dermophiidae	*Dermophis occidentalis*	LC	Fossorial				

Research topics.—Despite growing interest in research on herpetofauna globally, there is still disproportionate coverage of research topics and species as found by Troudet et al. (2017). We found the same for Costa Rican amphibian species. The most frequent research topics were ecology (n = 82, 25.07%) and behavior (n = 58, 17.7%), while evolution (n = 6, 1.83%) and genetics (n = 9, 2.75%) were the least represented. Anura was the only order addressed in all 14 topics assessed. Research on anurans was largely dominated by studies exploring ecology and behavior (Fig. 4). In addition to generating new knowledge, behavioral and ecological studies are highly important to conservation. Research on these topics helps us to understand the degree of susceptibility to declines or extinction (Walls and

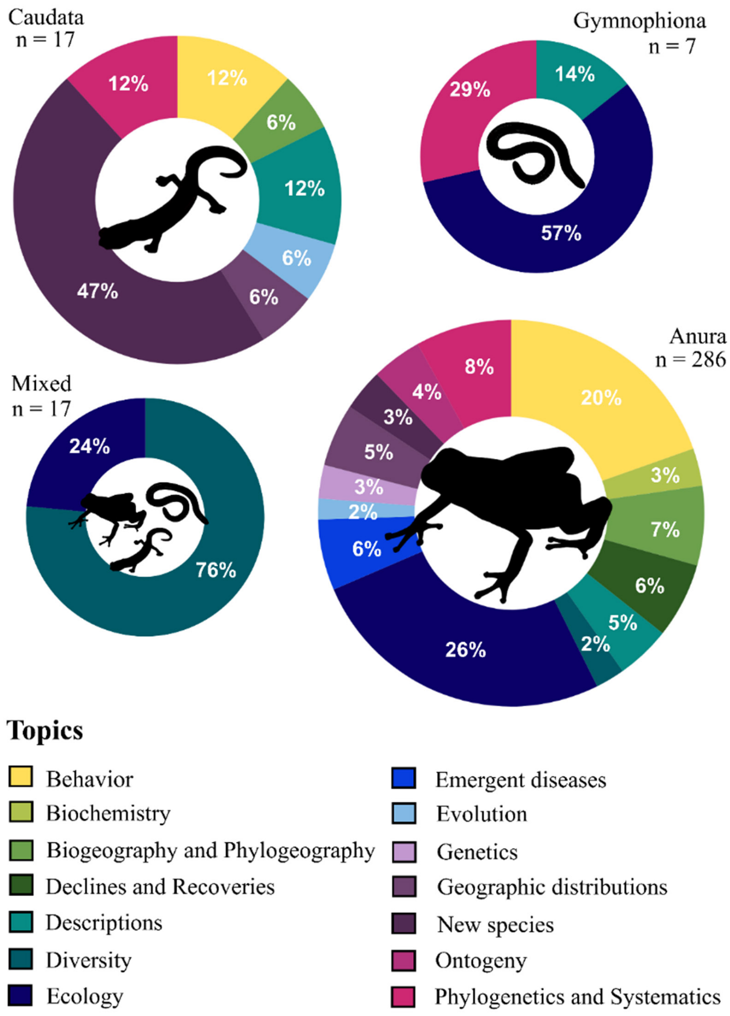

Figure 4. Percentage of publications on amphibians of Costa Rica organized by research topic for each amphibian order. See text for more extensive descriptions of topic categories.

Gabor 2019), the effects of habitat fragmentation on the behavior of dispersing individuals, and predation of local species by introduced species, to mention a few (Sutherland 1998). Comprehensive knowledge including other topics would allow better management and conservation decisions to be made, for example, in the design of monitoring programs or reintroduction strategies.

Among salamanders, a positive outcome during the study period was the description of several new species (Fig. 4), which represents an important contribution to the knowledge of Caudata in Costa Rica. Research beyond taxonomy, however, remains very limited, with little to no studies on ecology, ontogeny, emergent diseases, declines, genetics, or biogeography, highlighting major knowledge gaps for this group. In Gymnophiona, research was restricted to three topics: descriptions, ecology, and phylogeny. The 17 publications in which all three orders were represented focused exclusively on diversity and ecology (Fig. 4).

Red List categories.—Most studied species are listed as Least Concern (LC; n = 124; Fig. 3) by the IUCN. This aligns with the fact that 62% of Costa Rican amphibians fall into this category and are generally species that are easy to find. Amphibians categorized as lower risk are studied more extensively compared to their threatened counterparts elsewhere (Trimble and van Aarde 2010). Studying non-threatened species is essential because they are common organisms that can significantly influence trophic

Table 2. Number of sampled locations per Holdridge life zone and altitudinal belt (the symbol '–' indicates that the category does not occur).

		Holdridge life zones					
Elevational belt	Elevation (m)	Dry Forest	Moist Forest	Wet Forest	Rain Forest	Paramo	Total
Lowland	0–500	14	65	243	–	–	322
Premontane	500–1,000	–	60	289	105	–	454
Lower montane	1,000–1,500	–	2	74	150	–	226
Montane	1,500–2,000	–	0	2	33	–	35
Subalpine	> 2,000	–	–	–	–	0	0
Total		14	127	608	288	0	1,037

cascades (Chase 2003). They also represent a major source of biomass in certain ecosystems (Blaustein 1994; Schiesari et al. 2009) and play a crucial role in shaping ecosystem structure and processes (Trimble and van Aarde 2010). Furthermore, common non-threatened species can provide valuable insights into the biology and reproduction of less common species or those that are difficult to find, breed, or maintain in captivity.

In contrast, species in higher-risk categories remain largely understudied. The next most studied categories were Endangered (EN; n = 14) and Data Deficient (DD; n = 14; Fig. 3). Species not represented in publications included seven threatened species (VU, EN, CR), nine DD, and 12 LC species (Table 1). Threatened and Data Deficient species deserve increased attention, as both groups face elevated extinction risks, with DD species often being even more vulnerable than assessed taxa (Howard and Bickford 2014). Studying threatened species is crucial to prevent their extinction, and herpetologists working in Costa Rica should prioritize these taxa.

Research and publication trends suggest a biased focus on species that are common, charismatic, emblematic, or of general interest for research (Christie et al. 2021). This bias is not new: resource optimization often leads researchers to work with species that are easy to find, part of established populations, or located in conveniently accessible sampling sites (Silva et al. 2020). Although such practices facilitate the development of efficient research protocols, they may run counter to local and global conservation priorities (Bielby et al. 2006; Clark and May 2002; Ferronato 2019).

Geographic patterns.—We recovered 1,037 georeferenced sampling locations, covering 1.35% of the terrestrial surface of Costa Rica (51,100 km^2). Most were in the central mountain range and its Caribbean and Pacific foothills. Anuran sites spanned the country (2–3,395 m elevation, 566 km^2; 1.11%), while salamander (13–3,308 m elevation, 70 km^2; 0.014%) and caecilian (13–2,091 m elevation, 54 km^2; 0.011%) sites were scarce (Fig. 5). Sampling was concentrated in wet forest (n = 608), rainforest (n = 288), and moist forest (n = 127), with little attention to dry forests (n = 14), and no studies in Paramo ecosystems (Table 2). Elevationally, premontane zones had the highest number of records (n = 454), followed by lowland (n = 322) and lower montane zones (n = 226). In contrast, montane areas were strongly underrepresented, with only 35 records, and no sampling was reported for the subalpine belt (Table 2).

Only 42.3% of sites were within protected areas, while 57.7% were outside. Of 147 terrestrial protected areas, only 47 had at least one sampling site (Supplemental Information Table S3). The most studied locations were La Amistad International Park, a binational protected area shared with Panama and the largest national park in the country, and La Selva Research Station, a well-known private natural reserve with excellent infrastructure and worldwide institutional links. While La Amistad spans nearly 200,000 ha in Costa Rica (and a similar area in Panama), La Selva covers only about 1,600 ha. This sharp contrast in area further underscores the disproportionate representation of La Selva in research efforts. This overrepresentation of a small number of study locations has been noted in other research outside of Costa Rica, often due to the presence of known populations, ideal research conditions, security, and easy access (Amano and Sutherland 2013). Additionally, some locations have been frequently revisited by primary investigators and their students over many years, resulting in

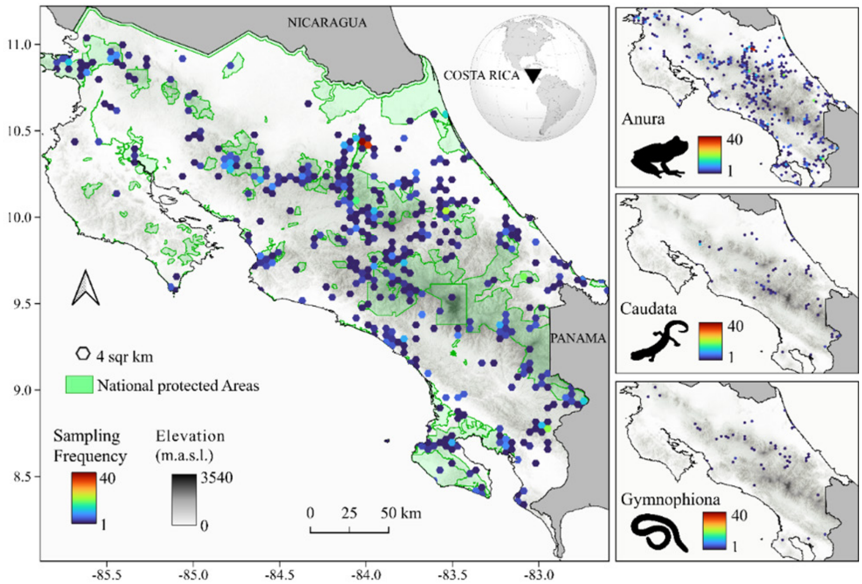

FIGURE 5. Overall and by-order sampling locations of amphibians across Costa Rica reported in research literature from 2000–2022. Dot colors refer to sampling frequency. Latitude and longitude (decimal degrees) are shown on the bottom and left side of the left panel, respectively.

extensive data about specific locations or species, e.g, *O. pumilio* from Hitoy Cerere (Meuche et al. 2013; Pröhl 1997, 2005; Pröhl and Berke 2001; Staudt et al. 2010).

When examining the sampling locations reported for specific orders, efforts were notably higher for anuran species. In contrast, vast regions of the country remain unexplored for Caudata species and especially Gymnophiona. Spatial research gaps are a common issue in ecological research, posing a significant challenge for conservation planning (Brito 2008). Understanding population dynamics requires a geographical context, and it is essential to focus research efforts on less-studied areas of the country, particularly in national parks and reserves where biodiversity is protected, and infrastructure is available but is largely underused.

Institutional and collaborative patterns.—Bibliometric analyses showed that among all author affiliations, researchers were more frequently associated with foreign institutions (67.3%) than with Costa Rican institutions (32.8%). Consistently, most publications appeared in international journals (297, 90.8%), with only 30 papers (9.2%) published in Costa Rican journals, and English predominated as the language of publication (97.8%). While this reflects the international scope of the research, it may also indicate limited accessibility for local stakeholders, students, and practitioners. Including Spanish-language abstracts or promoting journals that publish in both English and Spanish would help broaden access and facilitate the use of scientific information in decision-making and education at the national level. Notably, a growing number of Costa Rican researchers have established careers abroad, and their participation is reflected in publications affiliated with foreign institutions, underscoring the national contribution to international research.

Collaborations involved 236 institutions from 33 countries, including universities, research institutes, and non-governmental organizations. During the study period, the Universidad de Costa Rica (UCR), a national public university, had the highest scientific productivity (Supplemental Information Fig. S1). It was followed by the University of Veterinary Medicine Hannover in Germany (TiHo), and then by other Costa Rican and foreign institutions, including the Universidad Nacional (UNA), Florida International University (FIU), the Universidad Autónoma de Mexico (UNAM), and the University of California (UC).

At the country level, the U.S. showed the strongest collaboration link with Costa Rican institutions, followed by Mexico (Fig. 6). In terms of publication output, the U.S. ranked first, Costa Rica second, and Germany third. While Germany contributed substantially to the total number of studies, its collaboration with Costa Rican institutions was comparatively lower. Collaborating with institutions

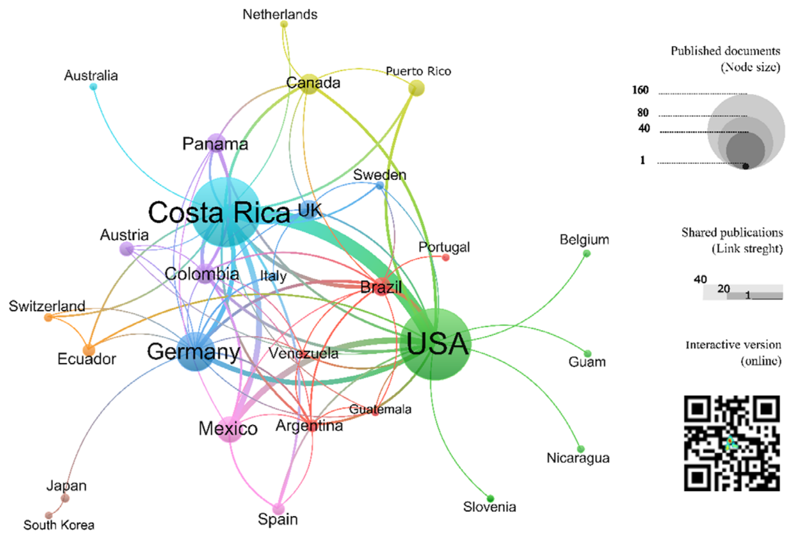

Figure 6. Collaboration network among countries contributing to research publications on Costa Rican amphibians between 2000 and 2022. Node size is proportional to the number of publications from each country, and the width of the connecting lines (link strength) represents the number of co-authored publications between countries. Scan the QR code to access an interactive version of the figure.

in other countries is essential for continuing to gather information about amphibians in Costa Rica, especially considering the limited national research budget and the small number of institutions and researchers dedicated to this field.

The absence of an army, a well-educated population, and access to drinking water are among the many advantages that make Costa Rica appealing to researchers globally. Costa Rica, a small country rich in biological diversity, is recognized for its natural tourism branding and innovative environmental policies (Murillo 2014). Notably, the government protects 25% of the territory for conservation purposes (Sistema Nacional de Áreas de Conservación 2022).

Future research priorities.—Research efforts in Costa Rica are uneven across taxa, topics, and geography. Salamanders remain poorly studied despite their high diversity and conservation concerns. Environmental DNA (eDNA) could provide valuable information for these species. Although not novel worldwide, this approach remains promising and underused in Costa Rica, particularly for salamanders and caecilians that are difficult to detect with traditional survey methods (Torresdal et al. 2017). Greater efforts are needed for the 44 species with only one publication and the 28 species with none (Table 1). Threatened and DD species must be prioritized for conservation. Topics such as ecology, distribution and niche models, evolution, phylogeography, and ontogeny are underexplored, particularly for Caudata and Gymnophiona. We recommend exploring additional protected areas that have not received adequate attention but harbor valuable ecosystems, such as Paramo, and provide access to lesser-known amphibian populations. Furthermore, we suggest focusing more on urban populations of amphibians that are adapting to survive in these settings and monitoring the impact of invasive species. In this regard, international partners could play a crucial role by supporting training opportunities for early-career Costa Rican researchers, facilitating long-term data accessibility, and co-developing research that aligns with local conservation challenges. Long-standing collaborations with international institutions, the establishment of biological stations that facilitate continuous fieldwork, and the creation of local academic networks providing training opportunities for students have been particularly influential in Costa Rica. While these experiences cannot be directly transferred to other national contexts, they highlight potential strategies to support the growth of herpetological research capacity in the region. Our synthesis highlights strong advances in amphibian research in Costa Rica but also reveals persistent biases and significant gaps. Addressing these will be critical to strengthening amphibian conservation in the country.

Acknowledgments.—We would like to express our gratitude to Jennifer Stynoski and Aldo Farah for their insightful comments that helped improve our manuscript.

Literature Cited

Amano, T., and W.J. Sutherland. 2013. Four barriers to the global understanding of biodiversity conservation: wealth, language, geographical location and security. Proceedings of the Royal Society B: Biological Sciences 280:20122649. https://royalsocietypublishing.org/doi/10.1098/rspb.2012.2649.

Amaral, C.R.L., A.C.S. Chaves, V.N.T. Borges Júnior, F. Pereira, B.M. Silva, D.A. Silva, A. Amorim, E.F. Carvalho, and C.F.D. Rocha. 2019. Amphibians on the hotspot: molecular biology and conservation in the South American Atlantic Rainforest. PLoS ONE 14:e0224320. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0224320.

Bielby, J., A.A. Cunningham, and A. Purvis. 2006. Taxonomic selectivity in amphibians: ignorance, geography or biology? Animal Conservation 9:135–143.

Barquero, M.D., and M. F. Araya. 2016. First record of the Greenhouse Frog, *Eleutherodactylus planirostris* (Anura: Eleutherodactylidae), in Costa Rica. Herpetology Notes 9:145–147.

Blaustein, A.R. 1994. Chicken Little or Nero's Fiddle? A perspective on declining amphibian populations. Herpetologica 50:85–97.

Brito, D. 2008. Amphibian conservation: are we on the right track? Biological Conservation 141:2912–2917.

Chase, J.M. 2003. Strong and weak trophic cascades along a productivity gradient. Oikos 101:187–195.

Christie, A.P., T. Amano, P.A. Martin, S.O. Petrovan, G.E. Shackelford, B.I. Simmons, R.K. Smith, D.R. Williams, C.F.R. Wordley, and W.J. Sutherland. 2021. The challenge of biased evidence in conservation. Conservation Biology 35:249–262.

Christoffel, R.A., and C.A. Lepczyk. 2012. Representation of herpetofauna in wildlife research journals. Journal of Wildlife Management 76:661–669.

Clark, J.A., and R.M. May. 2002. Taxonomic bias in conservation research. Science 297:191–192.

Di Marco, M., O. Venter, H.P. Possingham, and J.E.M. Watson. 2018. Changes in human footprint drive changes in species extinction risk. Nature Communications 9:4621. https://www.nature.com/articles/s41467-018-07049-5.

Falaschi, M., A. Melotto, R. Manenti, and G.F. Ficetola. 2020. Invasive species and amphibian conservation. Herpetologica 76:216–227.

Ferronato, B.de O. 2019. An assessment of funding and publication rates in herpetology. Herpetological Journal 29:264–273.

Fick, S.E., and R.J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Frost, D.R. 2024. Amphibian Species of the World: an online reference. Version 6.2 American Museum of Natural History, New York, USA. https://amphibiansoftheworld.amnh.org/index.php.

García-Rodríguez, A., G. Chaves, M. Wainwright, and A. Villegas. 2010. *Eleutherodactylus coqui* (Puerto Rican Coquí). Herpetological Review 41:320–321.

Gehanno, J.F., L. Rollin, and S. Darmoni 2013. Is the coverage of Google Scholar enough to be used alone for systematic reviews? BMC Medical Informatics and Decision Making 13:1–5. http://www.biomedcentral.com/1472-6947/13/7.

Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, et al. 2000. The Global decline of reptiles, déjà vu amphibians. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. BioScience 50:653–666.

Holdridge, L.R. 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.

Howard, S.D., and D.P. Bickford. 2014. Amphibians over the edge: silent extinction risk of data deficient species. Diversity and Distributions 20:837–846.

International Union for Conservation of Nature (IUCN). 2021. The IUCN Red List of Threatened Species, summary statistics. Version 2021–3. https://www.iucnredlist.org.

Leenders, T. 2017. Amphibians of Costa Rica. Cornell University Press, Ithaca, New York, USA.

López-Bedoya, P.A., P.D.A. Gutiérrez-Cárdenas, E.A. Cardona-Galvis, F.A. Edwards, D.P. Edwards, A. Blanco-Torres, and J.N. Urbina-Cardona. 2024. Knowledge shortfalls on amphibian diets in Colombia: future trends and challenges. Austral Ecology 49:e13600. https://onlinelibrary.wiley.com/doi/10.1111/aec.13600.

Luedtke, J.A., J. Chanson, K. Neam, L. Hobin, A.O. Maciel, A. Catenazzi, A. Borzée, A. Hamidy, A.

Aowphol, A. Jean, et al. 2023. Ongoing declines for the world's amphibians in the face of emerging threats. Nature 622:308–314.

Meiri, S., and D.G. Chapple. 2016. Biases in the current knowledge of threat status in lizards and bridging the 'assessment gap.' Biological Conservation 204:6–15.

Meuche, I., O. Brusa, K. Linsenmair, A. Keller, and H. Pröhl. 2013. Only distance matters – non-choosy females in a poison frog population. Frontiers in Zoology 10:29. http://www.frontiersinzoology.com/content/10/1/29.

Meuche, I., K.E. Linsenmair, and H. Pröhl. 2011. Female territoriality in the Strawberry Poison Frog (*Oophaga pumilio*). Copeia 2011:351–356.

Murillo, R. 2014. Assessing national destination-branding transformations: theory and application to Costa Rica's nature-based and medical tourism product-services. Pp. 71–109 *In* Tourists' Perceptions and Assessments. Woodside, A.C., and M. Kozak (Eds.). Emerald Group Publishing Limited, Bingley, UK.

Paluh, D.J., M.M. Hantak, and R.A. Saporito. 2014. A test of aposematism in the dendrobatid poison frog *Oophaga pumilio*: the importance of movement in clay model experiments. Journal of Herpetology 48:249–254.

Perianes-Rodriguez, A., L. Waltman, and N.J. van Eck. 2016. Constructing bibliometric networks: a comparison between full and fractional counting. Journal of Informetrics 10:1178–1195.

Pröhl, H. 1997. Patrón reproductivo en *Dendrobates pumilio* (Anura: Dendrobatidae). Revista de Biología Tropical 45:1669–1676.

Pröhl, H. 2005. Clutch loss affects the operational sex ratio in the Strawberry Poison Frog *Dendrobates pumilio*. Behavioral Ecology and Sociobiology 58:310–315.

Pröhl, H., and O. Berke. 2001. Spatial distributions of male and female Strawberry Poison Frogs and their relation to female reproductive resources. Oecologia 129:534–542.

R Development Core Team. 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rodríguez, A., N.I. Mundy, R. Ibáñez, and H. Pröhl. 2020. Being red, blue and green: the genetic basis of coloration differences in the Strawberry Poison Frog (*Oophaga pumilio*). BMC Genomics 2020 Apr 15;21(1):301. https://doi.org/10.1186/s12864-020-6719-5.

Rodríguez, J., G. Chaves, K. Neam, J. Luedtke, L. Carrillo, F. Bolaños, and Y. Matamoros (Eds.). 2020. Taller de evaluación de las necesidades de conservación de anfibios – Arca de los Anfibios y de la Lista Roja de la UICN: un esfuerzo para la segunda evaluación global de anfibios. Grupo de Especialistas en Anfibios y Grupo de Especialistas en Planificación para la Conservación, Unión Internacional para la Conservación de la Naturaleza, San José, Costa Rica. 40 p.

Roll, U., A. Feldman, M. Novosolov, A. Allison, A.M. Bauer, R. Bernard, M. Böhm, F. Castro-Herrera, L. Chirio, B. Collen, et al. 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. Nature Ecology and Evolution 1:1677–1682.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, Chicago, Illinois, USA.

Schiesari, L., E.E. Werner, and G.W. Kling. 2009. Carnivory and resource-based niche differentiation in anuran larvae: implications for food web and experimental ecology. Freshwater Biology 54:572–586.

Scott, J.M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T.C. Edwards, et al. 1994. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123:3–41.

Silva, A.F. da, A.C.M. Malhado, R.A. Correia, R.J. Ladle, M.V.C. Vital, and T. Mott. 2020. Taxonomic bias in amphibian research: are researchers responding to conservation need? Journal for Nature Conservation 56:125829. https://www.sciencedirect.com/science/article/pii/S1617138120300753.

Sistema Nacional de Áreas de Conservación (SINAC). 2022. Informe anual estadísticas SEMEC 2021: SINAC en números. Sistema Nacional de Áreas de Conservación (SINAC), Heredia, Costa Rica. 75 p.

Staudt, K., S.M. Ospina, D. Mebs, and H. Pröhl. 2010. Foraging behaviour and territoriality of the Strawberry Poison Frog (*Oophaga pumilio*) in dependence of the presence of ants. Amphibia-Reptilia 31:217–227.

Stynoski, J.L. 2009. Discrimination of offspring by indirect recognition in an egg-feeding dendrobatid frog, *Oophaga pumilio*. Animal Behaviour 78:1351–1356.

Sutherland, W.J. 1998. The importance of behavioural studies in conservation biology. Animal Behaviour

56:801–809.

Torresdal, J.D., A.D. Farrell, and C.S. Goldberg. 2017. Environmental DNA detection of the Golden Tree Frog (*Phytotriades auratus*) in bromeliads. PLoS ONE 12:e0168787. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0168787.

Trimble, M.J., and R.J. van Aarde. 2010. Species inequality in scientific study. Conservation Biology 24:886–890.

Troudet, J., P. Grandcolas, A. Blin, R. Vignes-Lebbe, and F. Legendre. 2017. Taxonomic bias in biodiversity data and societal preferences. Scientific Reports 7:9132. https://www.nature.com/articles/s41598-017-09084-6.

Urbina-Cardona, J.N. 2008. Conservation of Neotropical herpetofauna: research trends and challenges. Tropical Conservation Science 1:359–375.

Urbina-Cardona, J.N., and O. Flores-Villela. 2010. Ecological-niche modelling and prioritization of conservation-area networks for Mexican herpetofauna. Conservation Biology 24:1031–1041.

van Eck, N.J., and L.Waltman. 2014. Visualizing bibliometric networks. Pp. 285–320 *In* Measuring Scholarly Impact: Methods and Practice. Ding, Y., R. Rousseau, and D. Wolfram (Eds.). Springer International Publishing, Cham, Switzerland.

Wake, D.B., and M.S. Koo. 2018. Amphibians. Current Biology 28:R1237–R1241.

Walls, S.C., and C.R. Gabor. 2019. Integrating behavior and physiology into strategies for amphibian conservation. Frontiers in Ecology and Evolution 7:1–13.

Willink, B., E. Brenes-Mora, F. Bolaños, and H. Pröhl. 2013. Not everything is black and white: color and behavioral variation reveal a continuum between cryptic and aposematic strategies in a polymorphic poison frog. Evolution 67:2783–2794.

Winter, M., W. Fiedler, W.M. Hochachka, A. Koehncke, S. Meiri, and I. de la Riva. 2016. Patterns and biases in climate change research on amphibians and reptiles: a systematic review. Royal Society Open Science 3:160158. https://royalsocietypublishing.org/doi/10.1098/rsos.160158.

Supplemental Information: http://www.herpconbio.org/Volume_21/Issue_1/Esquivel_etal_2026_Suppl.pdf

Carolina Esquivel is an Associate Professor at Universidad Nacional, Heredia, Costa Rica. Her research focuses on the ecology, behavior, and conservation of amphibians, with a particular interest in antipredator strategies such as aposematism. (Photographed by Steve A. Stephens).

Jessica Gómez-Orozco is a recently graduated Biologist from Universidad Nacional, Heredia, Costa Rica. Her main interest is amphibian conservation. (Photographed by Rigoberto Zelaya).

Daniela Salazar-Sánchez is a recently graduated Biologist from Universidad Latina de Costa Rica, San José, Costa Rica. She is interested in amphibians, especially caecilians. (Photographed by Yarenis Villalobos).

Steve Allen Stephens-Cárdenas is an Associate Professor at Universidad Latina de Costa Rica, San José, Costa Rica. His interests include data management, statistics, populations and landscape genetics, and conservation. (Photographed by Carolina Esquivel).