ECOLOGICAL DETERMINANTS OF AMPHIBIAN AND REPTILE DIVERSITY: PATTERNS ACROSS SPATIAL SCALES

DETERMINANTES ECOLÓGICOS DE LA DIVERSIDAD DE ANFIBIOS Y REPTILES. PATRONES A TRAVÉS DE ESCALAS ESPACIALES

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Resumen.— Los patrones de biodiversidad son el resultado de procesos evolutivos y ecológicos que actúan por separado o en conjunto a diferentes escalas espacio-temporales. Los procesos específicos que afectan estos patrones de diversidad no serán los mismos para cada grupo taxonómico, ya que puede depender de las características específicas de cada grupo. En este trabajo, describimos los principales determinantes ecológicos que afectan los patrones de diversidad taxonómica y funcional de anfibios y reptiles en tres escalas espaciales: regional, paisaje y local. Además de las tendencias generales mencionadas en este documento, se destacan algunos vacíos de conocimiento que podrían servir para guiar futuros estudios que analicen la complejidad de los patrones de diversidad de anfibios y reptiles en todo el mundo.

Palabras clave.— Clima, composición del paisaje, estructura de la comunidad, interacciones bióticas, rasgos funcionales.

Abstract.— Biodiversity patterns result from evolutionary and ecological processes acting separately or in concert at different spatial and temporal scales. Since the importance of these processes may depend on taxon-specific characteristics, the ecological and evolutionary processes affecting diversity patterns will not be the same across distinct taxonomic groups. Here, we describe the major ecological determinants affecting both amphibian and reptile taxonomic and functional diversity patterns at three scales: regional, landscape, and local. In addition to the general trends presented herein, some knowledge gaps are highlighted to guide future studies that investigate the complexity of amphibian and reptile diversity patterns worldwide.

Keywords.— Biotic interactions, climate, community structure, functional traits, landscape composition.

Community diversity and its underlying ecological and evolutionary determinants have been a widely explored topic in community ecology (Weiher et al., 2011). Biological diversity is a complex phenomenon that comprises taxonomic, phylogenetic, and functional dimensions that are often used to measure distinct but complementary aspects (Magurran & McGill, 2011). Taxonomic diversity concerns the composition and relative abundance of species in a community (Whittaker, 1972), while phylogenetic diversity measures how many phylogenetically distinct lineages are present (Faith, 1992). Functional diversity focuses on the breadth of functional traits (i.e., measurable traits that impact fitness through their effects on growth, reproduction, and survival; Tilman, 2001; Violle et al., 2007). By exploring how these diversity dimensions change at different spatial and temporal scales and which ecological and evolutionary determinants might explain these patterns, we can take appropriate measures to conserve biodiversity in a changing world.

Biodiversity patterns are the result of key evolutionary and ecological processes acting separately or in concert at different spatial and temporal scales (Holt, 2003; Weiher et al., 2011; Pilowsky et al., 2022; Fig. 1). At broader scales, geological (e.g., plate tectonics) and evolutionary processes (e.g., speciation, adaptation, range expansion, evolutionary time; Mittelbach et al., 2007; Mittelbach & Schemske, 2015) promote the formation of regional species pools across the globe (Ricklefs, 1987; Ricklefs & Schluter, 1993). At finer scales, species' dispersal abilities (Holt, 2003), stochastic processes (e.g., ecological drift; Caswell, 1976; Hubbell, 2001), environmental filters and ecological interactions (Diamond, 1975; Abrams, 1983; Keddy, 1992; Weiher & Keddy, 1999) mainly determine which species from these pools may be present in local communities, although some studies have shown that allopatric speciation, colonization and local extinction may also play an important role on local diversity patterns (e.g., Pigot & Etienne, 2015). Differences in competitive ability, habitat and resource use determine species coexistence within local communities, and these interactions feedback to influence the biotic and abiotic environment (Chesson, 2000; HilleRisLambers et al., 2012; Mittelbach & Schemske, 2015). The importance of these processes is likely to depend on attributes, such as life history, physiology, trophic relationships, or behavior

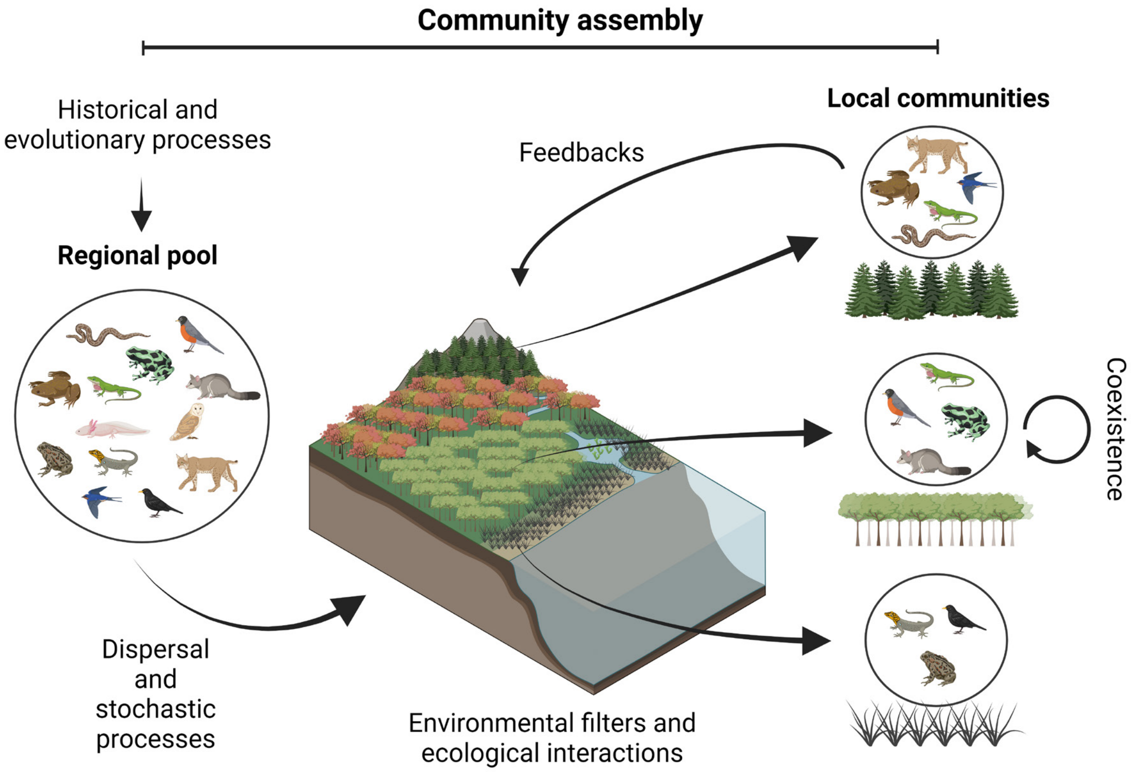

Figura 1. Diagrama que muestra los principales procesos ecológicos y evolutivos que determinan los patrones de diversidad y ensamblaje de comunidades a diferentes escalas espacio-temporales. A escalas gruesas, los procesos históricos y evolutivos promueven la formación de fuentes (*pools*) de especies particulares. A escalas más finas, la capacidad de dispersión de las especies, los procesos estocásticos, los filtros ambientales y las interacciones ecológicas determinan cuáles especies de estas fuentes pueden estar presentes en las comunidades locales. Las diferencias en la capacidad competitiva, utilización del hábitat y obtención de recursos de cada especie determina la coexistencia de las mismas dentro de las comunidades locales y estas interacciones, a su vez, pueden causar retroalimentaciones en el ambiente biótico y abiótico. Creado con BioRender.com.

Figure 1. Diagram showing the main ecological and evolutionary processes determining diversity patterns and community assemblies at different spatio-temporal scales. At broad scales, historical and evolutionary processes promote the formation of particular regional species pools. At finer scales, species' dispersal abilities, stochastic processes, environmental filters and ecological interactions determine which species from these pools may be present in local communities. Differences in competitive ability, habitat utilization and resource uptake determine the coexistence of species within local communities, and these interactions, in turn, may cause feedbacks in the biotic and abiotic environment. Created with BioRender.com.

that are shared by species of a specific taxonomic group. Thus, the specific ecological and evolutionary processes that affect diversity patterns are expected to vary across distinct taxonomic groups.

Evolutionary and ecological determinants of amphibian and reptile diversity patterns have been studied for a long time, and several important contributions have attempted to compile some of this vast amount of information. For instance, researchers have synthesized the major determinants affecting community structure of tropical tadpoles (Texeira-Borges & Duarte-Rocha, 2013), resource distribution in salamanders and newts (Vignoli et al., 2016), anthropic factors affecting amphibian and reptile communities (Cushman, 2006; Gardner et al., 2007; Hamer & McDonell, 2008; Thompson et al., 2015; Cordier et al., 2021), and determinants causing changes in diversity patterns along altitudinal gradients (McCain, 2010; Willig & Presley, 2016; Antonelli et al., 2018). Although important, these contributions mainly addressed specific determinants across a small number of scales, for a few taxonomic groups, or at restricted geographical ranges (Cushman, 2006; Gardner et al., 2017; Hamer & McDonell, 2008; Texeira-Borges & Duarte-Rocha, 2013; Thompson et al., 2015; Vignoli et al., 2016; Cordier et al., 2021). A more general synthesis of the major determinants affecting amphibian and reptile communities is needed to discern better the main processes acting at different spatial scales (or at least the most studied), and to identify knowledge gaps that need to be addressed to understand the community assembly of these groups better. Additionally, as each taxonomic group may be affected differently by these determinants and ecological processes, the synthesis described herein may be different from others performed with groups such as mammals or plants (e.g., Eiserhardt et al., 2011; Peixoto et al., 2018), and can be useful to either herpetologist starting their careers as well as experts who may use this information for future analyses.

In this perspective, we examine and describe the major ecological determinants affecting amphibian and reptile diversity patterns at regional, landscape, and local scales, according to what has been found in the literature (see Appendix 1: Methods; Appendix 2). Although scale boundaries may be subjective, most studies regard regional, landscape, and local scales as study areas spanning distances of > 200 km, 2 km – 200 km and < 2 km, respectively, with decreasing grain sizes (e.g., Pineda & Halffter, 2004; Urbina-Cardona et al., 2006; Hamer & Parris, 2011; di Virgilio et al., 2014; Iop et al., 2020; Barnagaud et al., 2021; Fonte et al., 2021). We delimited our perspective to the determinants of taxonomic and functional diversity patterns. Our aim is not to quantify the importance of each determinant at each scale, but rather to provide an overview of the main determinants having a positive or negative effect on amphibian and reptile diversity patterns. This is the first comprehensive synthesis of the main ecological factors affecting amphibian and reptile taxonomic and functional diversity patterns at multiple scales. We hope this perspective will prove useful as a guide for conservation, resource management and decision making, as well as a basis for ecologists aiming to investigate amphibian and reptile communities further.

REGIONAL SCALE: THE KEY ROLES OF HISTORY, CLIMATE, AND TOPOGRAPHY

Amphibian and reptile diversity patterns in a particular region are influenced primarily by the size and composition of regional pools, which differ from one region to another depending on their evolutionary histories and the interplay between speciation, extinction and dispersal events (e.g., Wiens, 2007; Pyron & Burbrink, 2011; Belmaker & Jetz, 2012; Pyron, 2014; Llorente-Culebras et al., 2021; Zamora-Marín et al., 2021; Fig. 1). For example, greater amphibian diversification in tropical regions seems to be explained by a higher speciation rate or evolutionary time in the tropics, higher extinction in temperate regions and limited dispersal out of the tropics, compared with temperate regions (e.g., Wiens, 2007; Pyron & Wiens, 2013; García-Rodríguez et al., 2020). Locations under similar conditions, but in separate regions, may exhibit highly discrepant local species richness and composition if, for example, dispersal between regions is limited or the formation history of both regions are different (Höfer & Bersier, 2001; Harrison & Cornell, 2008; Pyron & Burbrink, 2014; He et al., 2017; Valente-Debien et al., 2019; Rivas et al., 2021). Local richness sometimes tends to be greater as regional pool richness increases (Ricklefs, 1987; Ricklefs & Schluter, 1993; Harrison & Cornell, 2008; Rabosky et al., 2019), nevertheless, this relationship is not always clear as both regional and local processes may interactively influence each other (e.g., trade-offs between ecological specialization and dispersal at local scales could influence regional diversity patterns; Gonçalves-Souza et al., 2013).

Species distributions and dispersal across regions are affected by biogeographical barriers, such as mountain ranges, oceans, and rivers. This has been observed in *Anolis* species from the Antilles, where changes in species composition and morphological characteristics across different islands are due, in part, to the history of the geologic formation of the archipelago (Losos, 1992; Harmon et al., 2005; Langerhans et al., 2006; Stuart et al., 2012). This has also been seen in snakes assemblages, where species richness on islands is explained by colonization of new lineages from mainland, which ultimately depends on island isolation (Pyron & Burbrink, 2014). More recent examples have shown that distinct anuran and reptile communities exist on either sides of the Madeira River in the Amazon region and the São Francisco River in eastern Brazil (Dias-Terceiro et al., 2015; Marques-Peixoto et al., 2020; Gonçalves-Sousa et al., 2022), which attest the effects of smaller barriers on diversity patterns. Thus, these barriers may represent important determinants of diversity changes across regions that will depend on amphibians and reptiles limited dispersal capacities (e.g., Vitt & Caldwell, 2014; Arreortúa-Martínez, 2020; Brocka, 2020) and random events (e.g., ecological drift; Caswell, 1976; Hubbell, 2001).

Regional amphibian and reptile diversity patterns are mostly influenced by climatic factors and water-energy dynamics. Most studies agree that, in general, regions with higher average annual temperatures and precipitation tend to host greater taxonomic richness (Barnosky et al., 2001; Soares & Brito, 2006; Aragón et al., 2009; Laurencio & Fitzgerald, 2010; Qian & Kissling, 2010; di Virgilio et al., 2014; Kafash et al., 2020; Pinkert et al., 2020; Fonte et al., 2021; Liang et al., 2022; Raz et al., 2023) and functional diversity (Jiménez-Robles et al., 2017; García-Llamas et al., 2019; Ochoa-Ochoa et al., 2019; Barnagaud et al., 2021; Fonte et al., 2021; Castaño-Quintero et al., 2022) in both groups, although some exceptions are observed in salamanders, which tend to be more diverse in temperate regions with lower temperatures and higher precipitation rates (e.g., Kozak & Wiens, 2012; Gould et al., 2017). Both groups are highly dependent of water and energy inputs (Qian et al., 2007; Whittaker et al., 2007; Veetas et al., 2019), nevertheless, reptiles seem to be mostly affected by the amount of solar energy, usually measured as potential evapotranspiration, hours of sunshine, or minimum temperature (Barnosky et al., 2001; Hawkins et al., 2003; Rodríguez et al., 2005; Qian et al., 2007; Whittaker et al., 2007; Qian, 2010; Liang et al., 2022), while amphibians are affected by solar energy, water availability and productivity, measured as actual evapotranspiration, annual rainfall or the normalized difference vegetation index (Barnosky et al., 2001; Hawkins et al., 2003; Rodríguez et al., 2005; Qian et al., 2007; Whittaker et al., 2007; Qian, 2010; Gouveia et al., 2013; Zhang et al., 2017). Therefore, reptile diversity seems to be more constrained by energy inputs, while amphibian diversity by both water and energy inputs (Qian et al., 2007; Whittaker et al., 2007; Veetas et al., 2019).

Some of the patterns described above may be explained by amphibians' and reptiles' physiological and reproductive requirements (Vitt & Caldwell, 2014). For reptiles, temperature and the amount of solar energy are important factors for physiological functions such as locomotion, growth, and reproduction (Wang et al., 2016), and some species with specific thermal preferences may not prevail in regions with colder or extremely high temperatures (e.g., García-Llamas et al., 2019; García-Porta et al., 2019). For amphibians, precipitation and water availability are key for reproduction, as reflected by a greater diversity of reproductive modes in regions with higher precipitation rates (da Silva et al., 2012; Ochoa-Ochoa et al., 2019), especially of species that depend on lentic and lotic water bodies, or phytotelmata, for reproduction (e.g., Jiménez-Robles et al., 2017; Fonte et al., 2021). These patterns are also explained by a greater diversity of feeding guilds and habits, as well as smaller body sizes, in warmer regions for amphibians (e.g., García-Llamas et al., 2019; Rubalcaba et al., 2019; Fonte et al., 2021) or by changes in body sizes and activity patterns along climatic gradients for reptiles (e.g., species with bigger body sizes and diurnal activity in colder regions; Barnagaud et al., 2021; Rubalcaba et al., 2019, 2023).

Since climatic factors are important determinants of amphibian and reptile diversity, regions with higher aridity levels may harbor both amphibian and reptile communities with poorer functional diversity, due to ecological filters, or less functional redundancy, due to higher competition between functionally similar species (e.g., Ochoa-Ochoa et al., 2019; Gonçalves-Sousa et al., 2022). Nevertheless this may not be necessarily true for squamates, as some arid regions may have hyper-diverse communities with functionally-similar species (Wiens et al., 2012; Vidan et al., 2019). This is the case for Australian desert lizard communities which are outstandingly rich in comparison to other arid regions (e.g., North American, Kalahari, or Atacama deserts; Pianka, 1969; Pianka, 1971; Pianka, 1972, Pianka, 1973; Roll et al., 2017; Vidan et al., 2019; Tejero-Cicuéndez et al., 2022), where different ecological and evolutionary mechanisms have been proposed (e.g., greater diversification in larger geographic areas, higher evolutionary time and rate, effects of deep time environmental dynamics; James & Shine, 2000; Tejero-Cicuéndez et al., 2022).

Topographic factors in most regions are also related with amphibian and reptile taxonomic and functional diversity patterns. Regions with greater topographic heterogeneity tend to harbor higher taxonomic and functional diversity (Laurencio & Fitzgerald, 2010; McCain, 2010; Kozak & Wiens, 2012; Gould et al., 2017; Antonelli et al., 2018; Barnagaud et al., 2021; Liang et al., 2022; Rivera-Reyes, 2022), since they promote a higher number of vegetation types and land use covers (Nogués-Bravo & Martínez-Rica, 2004; Soares & Brito, 2006; Qian & Kissling, 2010; Muñoz et al., 2016; García-Llamas et al., 2018; Barnagaud et al., 2021), more complex hydrographic networks (Soares &

Brito, 2006; Vera et al., 2011; Muñoz et al., 2016), and diverse microclimatic conditions (Qian & Kissling, 2010), providing a broader ecological space for more species and promoting higher diversification rates (e.g., García-Rodríguez et al., 2020; García-Rodríguez et al., 2021). For example, amphibians dependent on lentic water bodies for reproduction may be more abundant in lower elevations, while species with direct development and terrestrial reproductive stages, in higher elevations (Jiménez-Robles et al., 2017). Slope variability can favor the presence of amphibian and reptile species with different dispersal or movement abilities that may use complementary resources (García-Llamas et al., 2019), while a higher number of vegetation types in more topographical heterogeneous regions may allow the prevalence of reptile species with different habits (Barnagaud et al., 2021), increasing functional diversity.

At the regional scale, land use change seems to be a relevant driver, as found by some authors (Ribeiro et al., 2009; Torres et al., 2014; Marsh et al., 2016; de Solan et al., 2018; García-Llamas et al., 2019; Gherghel et al., 2019; Barnagaud et al., 2021; Dehling & Dehling, 2023), nevertheless, it seems that the effects of climatic conditions and topography tend to be stronger (e.g., Keil et al., 2012; Lin et al., 2020; Barnagaud et al., 2021). Despite of this, few studies have still found a significant effect of land use change on amphibian and reptile diversity patterns at the regional scale (e.g., Ribeiro et al., 2009; Marsh et al., 2016; de Solan et al., 2018; García-Llamas et al., 2019; Barnagaud et al., 2021). For instance, a lower taxonomic and functional diversity have been observed in regions with a higher urbanization (de Solan et al., 2018; Barnagaud et al., 2021) and agricultural intensification (Ribeiro et al., 2009; Marsh et al., 2016; García-Llamas et al., 2019; Barnagaud et al., 2021). Land use change transforms heterogeneous and structurally complex land covers (e.g., forests) into more homogeneous ones (e.g., crops), reducing the ecological available space that can be used by functionally distinct species (e.g., Berriozabal-Islas et al., 2017; *see Local scale*). Species that tend to be more affected include those characterized as low fecundity, large-bodied (Barnagaud et al., 2021), omnivorous, tree-dwelling and diurnal (García-Llamas et al., 2019), while other species traits show a more complex pattern (e.g., García-Llamas et al., 2019). As most of these changes occur at smaller scales (e.g., *see Landscape and Local scales*) it is possible that the effect of land use change on diversity patterns at smaller scales are reflected at broader scales.

Biotic interactions affecting diversity patterns at a local scale are also reflected at the regional scale, specifically as non-random co-occurrence patterns. For example, *Plethodon* salamanders in eastern United States, and Pelomedusidae turtle communities in sub-Saharan Africa, are non-randomly structured according to body size, suggesting underlying mechanisms of competition or emergent neutrality that creates clusters of functionally redundant species (Adams, 2007; Luiselli et al., 2021). Snake communities seem to also be structured by competition, and species coexistence can be explained by food resources in tropical regions, and by available micro-habitat partitioning in temperate regions (Luiselli, 2006a). Nevertheless, other studies have found that the effects of biotic interactions on diversity are only detectable at much smaller scales (Rabosky et al., 2007; Aloise et al., 2015), or that some taxonomic groups may be unaffected by competitive mechanisms (e.g., most turtles communities; Luiselli, 2006b), suggesting that the relevance of climate, biotic interactions and other processes (e.g., stochastic processes) may vary between regions or taxa, depending on the context.

LANDSCAPE SCALE: THE IMPORTANCE OF HABITAT COMPOSITION AND CONFIGURATION

Although climatic and topographic gradients tend to be less pronounced as the spatial scale is reduced, they still shape amphibian and reptile diversity patterns in most landscapes. For example, small elevational changes can produce variations in Amazonian lizard taxonomic diversity (e.g., ranges from 24 to 128 m a.s.l.; Marques-Peixoto et al., 2020) and in anuran taxonomic and functional diversity in Mexico and Ecuador (e.g., Pineda & Halffter, 2004; Jiménez-Robles et al., 2017). This may be explained by changes in temperature, relative humidity, and habitat structure along these gradients, which represent important determinants for many amphibians and reptiles at the local scale (e.g., Cabrera-Guzmán & Reynoso, 2012; *see Local scale*). These micro-climatic and topographic variations produce species composition turnover across landscapes (e.g., Jiménez-Robles et al., 2017; Fig. 2), for which more ecologically different species (e.g., different habits, feeding guilds; García-Llamas et al., 2019) may be expected in landscapes with more heterogeneous topographic and micro-climatic conditions.

Landscape composition and configuration (i.e., types of land cover or uses and their spatial arrangement across a landscape; Turner & Gardner, 2015) is one of the most important and best studied determinants of amphibian and reptile diversity patterns at the landscape scale (Cushman, 2006; Gardner et al., 2007; Hamer & McDonell, 2008; Thompson et al., 2015; Cordier et al., 2021). Highly heterogeneous landscapes that include a mix of different vegetation types tend to harbor a greater taxonomic and functional diversity (e.g., Atauri & Lucio, 2001; García-Llamas et al., 2018; García-Llamas et al., 2019), as more ecologically distinct

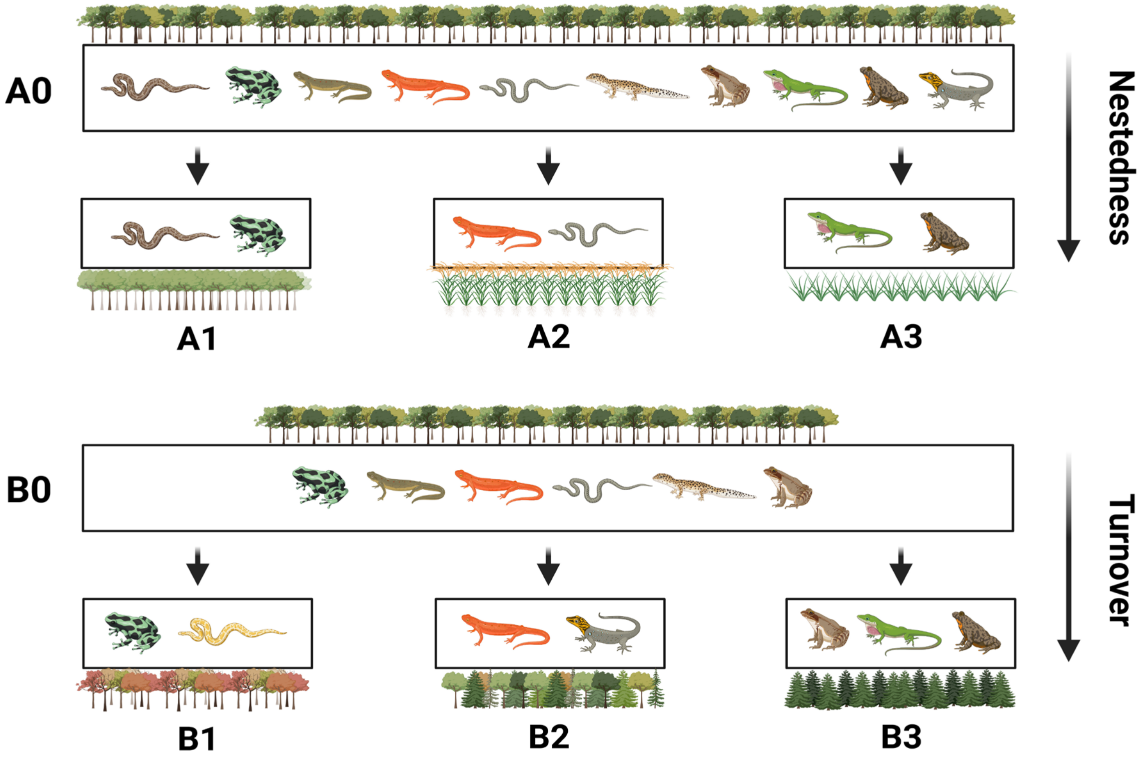

Figura 2. Ejemplo hipotético que describe patrones de recambio y anidamiento (Baselga, 2009) en dos paisajes diferentes (A y B). En el paisaje A se produce anidamiento, esto debido a que las comunidades A1-A3 son subconjuntos de la comunidad A0, la cual es más diversa. En este escenario, A0 representa un fragmento de bosque maduro grande, A1 un fragmento de bosque secundario, A2 un cultivo y A3 un pastizal. Por lo tanto, varias especies del fragmento de bosque maduro grande (A0) se pierden, y sólo algunas prevalecen en hábitats más perturbados (A1-A3). En el paisaje B se produce un recambio ya que todos los sitios tienen especies únicas, mientras que algunas son compartidas. En este escenario, cada sitio representa un tipo de bosque diferente que alberga principalmente especies únicas. Creado con BioRender.com.

Figure 2. Hypothetical example describing turnover and nestedness patterns (Baselga, 2009) in two different landscapes (A and B). In landscape A, nestedness occurs in which communities in A1-A3 are subsets of the broader community in A0. In this scenario, A0 represents a large mature forest fragment, A1 a secondary forest fragment, A2 a cropland and A3 a pasture. Therefore, species are lost from the large mature forest fragment (A0), and only some species prevail in more perturbed habitats (A1-A3). In landscape B, turnover occurs in which all sites have unique species while only some are shared. In this scenario, each site represents different forest types that harbor mainly unique species. Created with BioRender.com.

species may be present. In some cases, a mixture of natural and anthropic land uses increases amphibian and reptile diversity, as it favors both generalist and specialist species (e.g., Urbina-Cardona et al., 2006; Guerra & Aráoz, 2015; Berriozabal-Islas et al., 2017; Ferrante et al., 2017; Branoff & Campos-Cerqueira, 2021). Nevertheless, most studies coincide that the increase of anthropic land uses diminishes taxonomic (Pillsbury & Miller, 2008; Canessa & Parris, 2013; Leavitt & Fitzgerald, 2013; Michael et al., 2016; Sawatzky et al., 2019; Iop et al., 2020; Albero et al., 2021) and functional diversity (Almeida-Gomes et al., 2019), as it leads to the loss of some specialist species (e.g., Berriozabal-Islas et al., 2017; *see Local scale*). It is yet unclear what factors give rise to these contrasting patterns, although it may reflect the specific micro-climatic and micro-habitat characteristics of the anthropic land uses (*see Local scale*). For example, landscapes that have a greater diversity of anthropic land uses (e.g., different types of crops; Carpio et al., 2016; Collins & Fahrig, 2017) with greater structural complexity (Pineda & Halffter, 2004; Mendenhall et al., 2014; Guerra & Aráoz, 2015; Ferrante et al., 2017) and less contrast with the natural landscape composition (Deans & Chalcraft, 2016; Ryberg & Fitzgerald, 2016) may have a greater amphibian and reptile diversity.

The configuration of natural and modified land uses throughout human dominated landscapes help maintain amphibian and reptile diversity. For example, large, regular-shaped natural vegetation remnants (i.e., fragments) host a high taxonomic (Bell & Donnelly, 2006; Cabrera-Guzmán &

Reynoso, 2012; Leavitt & Fitzgerald, 2013; Russildi et al., 2016; Suárez et al., 2021; Schivo et al., 2023) and functional diversity (Almeida-Gomes et al., 2019; Palmeirim et al., 2021) in both groups. This is mainly attributed to a greater environmental and structural heterogeneity (Inger & Colwell, 1977; Almeida-Gomes et al., 2019), which allows ecologically different species to persist, especially those with specific arboreal or rheophilic (i.e., that preferred to live in lotic water bodies) habits, heliophobic thermoregulation modes (i.e., species that avoid direct exposure to solar radiation), specific reproductive modes (e.g., anurans depositing eggs on vegetation over standing water bodies) or species not-resistant to desiccation (Watling & Braga, 2015; Almeida-Gomes et al., 2019; Palmeirim et al., 2021). Also, large fragments are colonized more easily, allowing species to have larger population sizes and lower extinction rates (Arrhenius, 1921; Almeida-Gomes et al., 2022). However, small fragments with a combined area equivalent to a large fragment may host greater species diversity, as both generalist and specialist species may use them (Fahrig, 2020). As such, several authors have emphasized the importance of conserving small fragments throughout landscapes affected by land use change (Lomolino, 2000; Lindenmayer, 2019; Wintle et al., 2019; Hamer, 2021).

A higher density and connectivity of small natural vegetation remnants are also correlated with a higher amphibian and reptile taxonomic and functional diversity (e.g., Mazerolle & Villard, 1999; da Silva et al., 2011; Almeida-Gomes & Rocha, 2014; Mendenhall et al., 2014; Ghosh & Basu, 2020; Ramírez-Arce et al., 2022), since they may facilitate dispersal to and occupation in degraded landscapes. The same is true for water bodies, in which greater density and connectivity permit higher amphibian taxonomic (Lemckert & Mahony, 2010; Hamer & Parris, 2011; Vera et al., 2011; le Viol et al., 2012; Bounas et al., 2020; Ghosh & Basu, 2020) and functional diversity (Ribeiro et al., 2017), as well as a higher aquatic snake taxonomic diversity (Vogrinc et al., 2018). For instance, the diversity of amphibian activity patterns, habits, and reproductive modes reduces the further the distance to water bodies (Ribeiro et al., 2017), reflecting their importance for rich amphibian communities to persist. These landscape elements may be important for metapopulation and metacommunity dynamics, serving as sources for sink habitats, such as anthropic land uses (Richter-Boix et al., 2007; Ryberg & Fitzgerald, 2016; Rosas-Espinoza et al., 2022), or as biological corridors between large vegetation remnants. In this sense, anthropic land uses with greater structural complexity and less contrast with respect to natural land covers is also beneficial to metapopulation and metacommunity dynamics by being more permeable matrices for dispersal (Deans & Chalcraft, 2016; Ryberg & Fitzgerald, 2016; Hernández-Ordóñez et al., 2019).

Biotic interactions that affect diversity patterns at local scale are also reflected at the landscape scale, as species occurrences throughout the landscape can be influenced by interactions, such as competition. For instance, in the United States the rattlesnake species *Crotalus horridus* is less likely to use large, forested areas that also contain *Crotalus adamanteus* snakes (Steen et al., 2014). This is due to trophic niche overlap between the two species and probably a higher competitive hierarchy of *Crotalus adamanteus*. When other land uses are present, both co-occur more often (Steen et al., 2014), implying that landscape characteristics also influence species interactions. Competition can also structure communities of amphibians in low-productivity habitats in Brazil (Huckembeck et al., 2020) and of snakes in degraded land uses in Nigeria (Luiselli, 2006c), which are presumed to have lower resource availability. Nevertheless, some studies have found that amphibians communities in the Chihuahuan desert are mainly structured by environmental differences between land covers, and not by competition (Schalk et al., 2015). This suggests that the relevance of landscape characteristics, environmental filters and biotic interactions may change depending on the biogeographical context of each landscape.

LOCAL SCALE: THE IMPACT OF MICRO-HABITAT CHARACTERISTICS AND BIOTIC INTERACTIONS

Most anthropic land uses have a negative impact on amphibian and reptile communities (Newbold et al., 2015, 2018, 2020). A lower taxonomic and functional diversity is observed in such land uses in comparison with natural land covers (Cushman, 2006; Cagle, 2008; Canessa & Parris, 2013; Trimble & van Aarde, 2014; Carpio et al., 2016; Hölting et al., 2016; Russildi et al., 2016; Berriozabal-Islas et al., 2017; Hernández-Ordóñez et al., 2019; Ghosh & Basu, 2020; Cordier et al., 2021; Rosas-Espinoza et al., 2022; Schivo et al., 2023), although similar values have been recorded in some instances (e.g., shade-grown coffee, cacao crops or agricultural *marais*; Heinen, 1992; Pineda & Halffter, 2004; Wanger et al., 2009; Brüning et al., 2018; Dehling & Dehling, 2023). Even though a clear pattern is not always observed for how different traits may change (e.g., Ribeiro et al., 2017; Rosas-Espinoza et al., 2022), some studies suggest that species lost from anthropic land uses tend to be large-sized anuran species (Ribeiro et al., 2017) with arboreal habits, specific reproductive modes (e.g., reproduction in streams; Almeida-Gomes et al., 2019; Baffa-Trasci et al., 2020) and smaller clutch sizes (Jiménez-Robles et al., 2017), as well as heliophobic reptiles species with larger body sizes, that depend on water bodies (Palmeirim et al., 2021) and specialized diets (Berriozabal-Islas et al., 2017). A select few generalist species may prevail in these perturbed habitats, however, producing a nested pattern where species are gradually lost from highly-rich natural environments to poorer, anthropic ones (e.g., Berriozabal-Islas et al., 2017; Almeida-Gomes et al., 2019; Branoff & Campos-Cerqueira, 2021; Dehling & Dehling, 2023; Fig. 2), although species turnover may also be observed due to some unique species occurring only in degraded habitats (e.g., Jiménez-Robles et al., 2017; Rosas-Espinoza et al., 2022; Fig. 2).

The fact that some anthropic land uses have similar amphibian and reptile diversity values as do natural land covers (Pineda & Halffter, 2004; Mendenhall et al., 2014; Guerra & Aráoz, 2015; Ferrante et al., 2017; Branoff & Campos-Cerqueira, 2021; Rosas-Espinoza et al., 2022) may be explained by their structural heterogeneity. For example, shade coffee, cacao and palm heart plantations have a more complex vegetation structure and leaf litter depth than other anthropic land uses, such as intensive croplands and pastures, creating more available ecological space that can be used by ecologically different species (Heinen, 1992; Pineda & Halffter, 2004; Kurz et al., 2014). Moreover, changes in vegetation structure caused by wood extraction (Patrick et al., 2006; MacNeil & Williams, 2014; Eyre et al., 2015; Hölting et al., 2016; Muñoz et al., 2021), fire regimes (Rochester et al., 2010; Santos & Cheylan, 2013) or cattle (Kutt et al., 2012; Ferrante et al., 2017), presence of pollution (Taylor & Fox, 2001; Suárez et al., 2021) or introduced grasses (Schlesinger et al., 2020), and direct mortality by humans may cause the local extinction of some reptile species in natural land covers, reducing taxonomic and functional diversity.

Micro-climatic and micro-habitat characteristics, thus, seems to explain much of the diversity patterns observed at broader scales and within localities (e.g., Bars-Closel et al., 2017; Zamora-Marín et al., 2020). For example, greater taxonomic diversity is usually observed in sites and seasons of the year with higher relative humidity and intermediate temperatures (e.g., Cabrera-Guzmán & Reynoso, 2012; da Silva et al., 2012; Villa et al., 2019), since low humidity and extreme temperatures can cause desiccation and create habitats that exceed reptile and amphibian thermal tolerances. Elevation and slope are also important factors, and a greater taxonomic (Laurencio & Fitzgerald, 2010; Qian & Kissling, 2010; Cabrera-Guzmán & Reynoso, 2012; Dias-Terceiro et al., 2015; Muñoz et al., 2016; de Solan et al., 2018) and functional diversity (Jiménez-Robles et al., 2017; de Solan et al., 2018; García-Llamas et al., 2019; Marques-Peixoto et al., 2020) are observed at lower elevations and in terrains with lower slopes (although intermediate and high elevations may also have high species richness depending on the region and context; McCain, 2010; Kutt et al., 2011). This may be explained by the correlation between elevation and some important micro-climatic conditions for amphibians and reptiles as explained above (e.g., temperature, relative humidity), as well as a greater prevalence of lentic water bodies in lowlands, which are important for amphibian reproductive modes that rely on water bodies for egg deposition, or habitat-specific reptiles dependent of high humidity levels (e.g., Jiménez-Robles et al., 2017; Ribeiro et al., 2017; Marques-Peixoto et al., 2020). Also, lower slopes may represent a less energetic cost for most species' movements (e.g., those with smaller body sizes), and may have a complex vegetation structure (e.g., more large trees and woody elements; Martínez-Ramos et al., 1988; Cabrera-Guzmán & Reynoso, 2012) and more stable daily temperature patterns (Pianka, 2000). For semiaquatic environments, higher levels of oxygenation (Weaver & Barret, 2017; Bounas et al., 2020), variable values of conductivity (de Oliveira & Eterovick, 2009; Hamer & Parris, 2011), longer hydroperiods (da Silva et al., 2012; Vogrinc et al., 2018; Atkinson et al., 2021), the presence of sandstone, stony or clay substrates (Lemckert & Mahony, 2010; Kret et al., 2015) and a higher proportion of natural vegetation (Sanchez et al., 2009; Lemckert & Mahony, 2010; Hamer & Parris, 2011; da Silva et al., 2012; Provete et al., 2014; Kret et al., 2015; Albero et al., 2021; Schivo et al., 2023; but see Skelly et al., 2014) have all been shown to promote greater taxonomic and functional diversity for amphibians and aquatic snakes. Water-body size may be also important (Sanchez et al., 2009; Lemckert & Mahony, 2010; da Silva et al., 2012; Provete et al., 2014; Baffa-Trasci et al., 2020; Albero et al., 2021; Schivo et al., 2023), as larger ponds usually provide more refuges and breeding sites for amphibians (although they may, in turn, harbor a greater number of predators, making some species more abundant in small, ephemeral water bodies; Wellborn et al., 1996; Richter-Boix et al., 2007; Sanchez et al., 2009). For terrestrial environments, sites with greater leaf-litter depths (Cabrera-Guzmán & Reynoso, 2012; Ochoa-Ochoa et al., 2014; Eyre et al., 2015), canopy cover (Pineda & Halffter, 2004; Urbina-Cardona et al., 2006; Behangana et al., 2009; Cabrera-Guzmán & Reynoso, 2012; Garda et al., 2012), herb, shrub, rocks or woody debris cover (Cabrera-Guzmán & Reynoso, 2012; Eyre et al., 2015; Rotem et al., 2020; Evans et al., 2019; Ramírez-Arce et al., 2021) and presence of large trees and structurally complex vegetation (Garda et al., 2012; Dias-Terceiro et al., 2015; Doherty et al., 2015; Michael et al., 2016; Goutte et al., 2017; Neilly et al., 2017; Marques-Peixoto et al., 2020) harbor greater amphibian and reptile taxonomic and functional diversity.

Biotic interactions are, perhaps, one of the most important determinants of species occurrence at the local scale (Diamond, 1975; Schoener, 1977; Bruno et al., 2003). Negative interactions, such as competition and predation, are important determinants of amphibian and reptile diversity patterns. For instance, the presence of predators, such as fish (Bounas et al., 2020), aquatic invertebrates (Richter-Boix et al., 2007) and salamanders (Sredl & Collins, 1991), in large-sized ponds can lead to a decrease in tadpole density in some species, affecting diversity patterns observed. Also, the presence of invasive species can decrease the abundance of native species through competition for similar food resources, as has been observed for anurans in aquatic ecosystems of the United States (Pilliod et al., 2010) and Spain (Richter-Boix et al., 2013). Differences in the competitive ability of species with overlapping niches may lead to competitive exclusion, but some mechanisms, such as niche partitioning, allow species to coexist (Winemiller & Pianka, 1990; Chesson, 2000; HilleRisLambers et al., 2012; Vignoli et al., 2016).

The capacity of amphibians and reptiles to partition multiple niche dimensions may allow species to coexist in many localities. For example, *Sceloporus* species in Mexico consume similar food resources, but substrate use between species tends to differ (Barbault et al., 1985). *Anolis* ecomorphs in the Antilles mainly differ from each other in the food resources they consume and the micro-habitats they use (Losos, 1994), while species within the same ecomorph group may differ in thermal preferences (i.e., substrates used for thermoregulation; Ingram et al., 2022). Lizard species in Australia have been observed to partition temporal (i.e., hours of activity), spatial (i.e., micro-habitats used), and trophic (i.e., food) niche dimensions, allowing a greater number of species to comprise a community (Pianka, 1973). Interestingly, temporal niche partitioning of acoustic activity may allow amphibians with similar micro-habitat and food preferences to reduce potential competition (Boquimpani-Freitas et al., 2007; Sanchez et al., 2009; but see Ochoa-Ochoa et al., 2021; Sugai et al., 2021). The same happens in space: stream noise promotes micro-habitat partitioning among anurans, where different species occupy sites at different distances from the stream (Carvajal-Castro & Vargas-Salinas, 2016). Niche partitioning among species is also possible due to differences in life history traits, such as reproductive activity, sexual maturity, and body size (López-Juri et al., 2015). Thus, the diversity of ecological preferences in amphibian and reptile communities plays an important role in species coexistence.

Although relatively less studied, facilitation (Bruno et al., 2003) seems to be an important diversity determinant that arise from modifications of the microhabitat. Ecological engineers (i.e., organisms that directly or indirectly control the resource availability for other species by modifying the physical environment; Pringle, 2008) can create appropriate environments for some amphibian and reptile species. For example, dam construction by beavers in the United States results in permanent aquatic habitats with a high diversity of breeding sites for several amphibian species (Cunningham et al., 2007; Romansic et al., 2020). Likewise, African elephants modify the vertical structure of the vegetation they feed on, creating a greater number of refuges for *Lygodactylus keniensis* lizards (Pringle, 2008). Other examples of facilitation include the use of bromeliads and leaf-cutter ant nests as refuges or oviposition sites in several anuran species (e.g., *Chiasmocleis antenori, Lithodytes lineatus, Oophaga pumilio, Osteocephalus fuscifacies, Smilisca baudinii*; Savage, 2002; Schlüter et al., 2009; Jiménez-Robles et al., 2017; Aguilar-Cruz et al., 2021; Fig. 3). Therefore, facilitation represents and important, but underrated, aspect that must be further explored.

The effects of interactions depend on micro-habitat characteristics and neutral processes. For example, higher resource availability, such as prey density, allows snake species in South Carolina, United States, to have a broader niche overlap without negative competition effects (Durso et al., 2013), while lower resource availability promotes higher trophic and spatial partitioning in chameleons in Nigeria and western Cameroon (Luiselli, 2006d). Variation in precipitation rates throughout the year modify temporal niche partitioning among anuran species in the Atlantic Forest of Brazil (Boquimpani-Freitas et al., 2007), with different acoustic activity patterns at each season of the year (but see Ochoa-Ochoa et al., 2021). At small scales, random events such as small disturbances, resource pulses or the arrival of a pregnant female to a given pond may have profound effects of the local diversity. Also, because small areas can only support relatively few individuals, demographic stochasticity is expected to determine population dynamics (Melbourne, 2012). Thus, random colonization, extinction and ecological drift are likely to regulate communities at small scales, allowing for coexistence and determining diversity (Martins et al., 2015). Therefore, biotic interactions, micro-habitat conditions, and stochastic processes seem to synergistically influence the structure of many amphibian and reptile communities.

CONCLUSIONS AND FUTURE PERSPECTIVES

In this perspective, we have described important ecological determinants explaining amphibian and reptile diversity patterns at distinct spatial scales (Table 1). Regional species pools and biogeographical barriers, in combination with climate, water-energy inputs and topographical gradients (e.g., temperature, precipitation, potential evapotranspiration, hours of sunshine, minimum temperature, actual evapotranspiration, annual rainfall, normalized difference vegetation index,

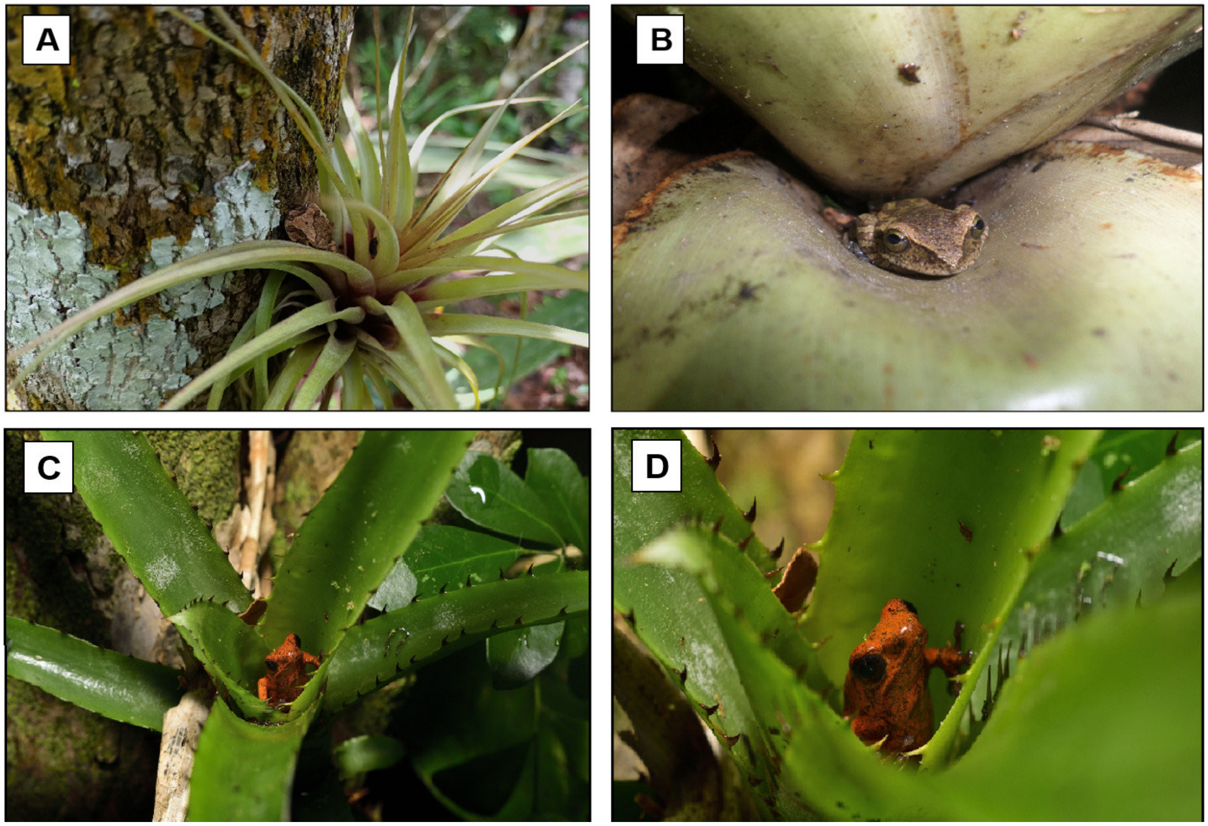

Figura 3. Ejemplos de interacciones positivas, como la facilitación. En A y B, mostramos imágenes del anuro *Smilisca baudinii* usando bromelias como refugio, mientras que en C y D, mostramos al anuro *Oophaga pumilio* usando bromelias como sitios de oviposición (es decir, sitios para el desarrollo de sus renacuajos). Fotos: A y B por Victor Hugo Colín Martínez y Yonatan Aguilar Cruz. Fotos: C y D por Leonardo Daniel Ponce Rosales.

Figure 3. Examples of positive interactions, such as facilitation. In A and B, we show images of the anuran *Smilisca baudinii* using bromeliads as a refuge, while in C and D, we show the anuran *Oophaga pumilio* using bromeliads as oviposition sites (i.e., sites for tadpole development). Photos: A and B by Victor Hugo Colín Martínez and Yonatan Aguilar Cruz. Photos: C and D by Leonardo Daniel Ponce Rosales.

topographic heterogeneity and slope variability), are important factors determining diversity patterns at the regional scale. At the landscape scale, micro-climatic and topographic variations in temperature, relative humidity or elevation, and landscape composition and configuration (e.g., land use change, landscape heterogeneity, density and connectivity of natural vegetation remnants and ponds), represent some of the main determinants of diversity patterns, although the effects of landscape composition (i.e., land use change) are often reflected at the regional scale. Finally, land use-change, micro-climatic conditions (i.e., temperature, relative humidity), micro-habitat characteristics (i.e., elevation, slope, water body characteristics, vegetation composition and structure), biotic interactions (e.g., competition) and facilitation are important determinants at the local scale, although the effects of interactions have also been observed at landscape and regional scales. The discussed determinants could be acting separately or in concert, and observed taxonomic and functional diversity patterns reflect the specific functional traits and niche requirements of amphibians and reptiles. Besides the general trends that we discussed throughout this perspective, we also identified several knowledge gaps that could be important to consider in order to guide future studies. These gaps are discussed in the rest of this section, along with the final conclusions.

Gaps at each spatial scale. At the regional scale, we observed that the effects of biogeographical barriers are important historical determinants of amphibian and reptile diversity patterns. Nevertheless, relatively few studies seems to have directly evaluated their effects (e.g., Dias-Terceiro et al., 2015; Marques-Peixoto et al., 2020; Gonçalves-Sousa et al., 2022), with most of them focusing on climatic and topographical influences (e.g., Soares & Brito, 2006; Laurencio & Fitzgerald, 2010; Qian & Kissling, 2010; di Virgilio et al., 2014; Jiménez-Robles et al., 2017;

Tabla 1. Síntesis de los principales determinantes de los patrones de diversidad de anfibios y reptiles en cada escala espacial. Los signos de más (+) y menos (-) reflejan la dirección del efecto de cada determinante en los patrones de diversidad taxonómica y funcional. La configuración del paisaje, las características del microhábitat de ambientes terrestres o semiacuáticos y las interacciones bióticas pueden tener efectos positivos o negativos en los patrones de diversidad, dependiendo de las condiciones específicas del paisaje/microhábitat o las interacciones examinadas. Para más detalles, consultar el texto.

Table 1. Synthesis of the main determinants of amphibian and reptile diversity patterns at each spatial scale. Plus (+) and minus (-) signs reflect the direction of the effect of each determinant on taxonomic and functional diversity patterns. Landscape configuration, semiaquatic and terrestrial environments' micro-habitat characteristics and biotic interactions may have positive or negative effects on diversity patterns, depending on the specific landscape/micro-habitat conditions or interactions examined. For more details, see the text.

Ecological determinants	Spatial scale		
	Regional	Landscape	Local
Historical factors			
Regional pools and evolutionary dynamics (+)	🟩		
Historical barriers: rivers, oceans, mountains (+)	🟩		
Climate and water-energy dynamics			
Macro-climatic conditions: Annual temperature and precipitation (+)	🟩		
Water-energy inputs: Potential and actual evapotranspiration, hours of sunshine, minimum temperature, normalized difference vegetation index, productivity (+)	🟩		
Micro-climatic conditions: Temperature and relative humidity (+)		🟩	🟩
Aridity levels (-)	🟩		
Topography			
Topographic heterogeneity: Variation in elevation, slope and topography (+)	🟩	🟩	
Elevation (-)			🟩
Slope (-)			🟩
Habitat structure			
Landscape compositional heterogeneity (+)	🟩	🟩	
Landscape configuration: Large vegetation remnants, density and connectivity of small vegetation remnants and ponds (+/-)		🟩	
Land use change: Perturbed land uses (-)	🟩	🟩	🟩
Semiaquatic environment's micro-habitat characteristics: Water bodies' morphology, level of oxygenation, conductivity, hydroperiod, and presence of sandstone/stony/clay substrates or natural vegetation (+/-)			🟩
Terrestrial environment's micro-habitat characteristics: Leaf-litter depth, canopy cover, herb/shrub/rocks/woody debris cover, and presence of large trees and structurally complex vegetation (+/-)			🟩
Small perturbations			
Wood extraction (-)			🟩
Fire regimes (-)			🟩
Grazing (-)			🟩
Pollution (-)			🟩
Introduced species (-)			🟩
Biotic interactions			
Competition (+/-)	🟩	🟩	🟩
Facilitation (+)			🟩

García-Llamas et al., 2019; Ochoa-Ochoa et al., 2019; Barnagaud et al., 2021; Fonte et al., 2021). Additionally, biotic interactions and land use change are mainly studied at the local scale, but their effects can be seen at the regional scale as well (e.g., Luiselli, 2006a, b; Adams, 2007; García-Llamas et al., 2019; Barnagaud et al., 2021; Luiselli et al., 2021). Therefore, more efforts are needed to address the effects of different kinds of biogeographic barriers and evolutionary processes, as well as land use change and biotic interactions, on amphibian and reptile diversity patterns at broader scales, particularly in topographically complex regions affected by anthropic activities.

At the landscape scale, we observed a predominant focus on investigating the impacts of landscape composition and configuration on amphibian and reptile diversity patterns, with a particular interest in the amount of habitat and its spatial arrangement in the landscape (e.g., Cushman, 2006; Gardner et al., 2007; Hamer & McDonell, 2008; Canessa & Parris, 2013; Leavitt & Fitzgerald, 2013; Thompson et al., 2015; Michael et al., 2016; Sawatzky et al., 2019; Iop et al., 2020; Albero et al., 2021; Cordier et al., 2021). Nevertheless, we believe that in the face of the ongoing land use change across the globe, more studies must also focus on evaluating which anthropic land uses (e.g., which kind of crops) could be less harsh for amphibian and reptile communities at different natural environments, as those with greater structural complexity or less contrast with the natural landscape composition may allow the presence of many different species (Pineda & Halffter, 2004; Mendenhall et al., 2014; Guerra & Aráoz, 2015; Deans & Chalcraft, 2016; Ryberg & Fitzgerald, 2016; Ferrante et al., 2017). This approach holds promise for devising innovative strategies that reconcile human economic development with biodiversity preservation, by selecting those anthropic land uses that produce less impact in particular landscapes. Additionally, while biotic interactions remain under-explored at this scale, they likely play a pivotal role in shaping species presence within the landscape. Thus, we advocate for the incorporation of biotic interactions, such as co-occurrence patterns, in landscape-level studies to provide a more comprehensive understanding of the ecological dynamics at play.

At the local scale, we observed that most studies evaluating biotic interactions seems to focus on competition, niche overlap and niche partitioning between species (e.g., Pianka, 1973; Boquimpani-Freitas et al., 2007; Richter-Boix et al., 2007; Pilliod et al., 2010; Durso et al., 2013; Richter-Boix et al., 2013; Ingram et al., 2022). Few studies, nevertheless, seems to have focused on facilitation, despite this likely being equally important in explaining species occurrences and diversity patterns (e.g., Cunningham et al., 2007; Pringle, 2008; Romansic et al., 2020), and virtually no study seems to concern on positive interactions such as mutualism or commensalism, at least from what was revised in this perspective. We suggest that more studies explore the role of these interactions at local and broader scales, with particular attention to facilitation and positive interactions.

The need for multi-scale studies. Processes across different scales are likely acting in concert. For example, specific micro-habitat characteristics, generally measured at the local scale, may explain diversity changes at the landscape scale (e.g., Mendenhall et al., 2014; Kurz et al., 2014; Rosas-Espinoza et al., 2022). Biotic interactions determine species occurrences at the landscape scale, while at the same time being influenced by changes in landscape and micro-habitat characteristics (e.g., Luiselli, 2006c; Boquimpani-Freitas et al., 2007; Durso et al., 2013; Steen et al., 2014). Exploring processes at a single scale may not be informative by itself, and could even produce unclear patterns. Thus, studies assessing patterns of amphibian and reptile diversity should be performed at multiple hierarchical scales in order to better understand the patterns observed. This could be done by measuring the same set of ecological determinants (and its relationships with taxonomic and functional diversity) at different extents and grains of analysis in order to identify the "scale of effect" of each determinant (i.e, the appropriate scale at which the ecological response is best predicted by a particular determinant; Wiens, 1989; Jackson & Fahrig, 2012; Jackson & Fahrig, 2015).

The importance of selecting appropriate functional traits. Taxonomic and functional diversity are usually correlated (de Bello et al., 2021), and therefore, most studies showed that both dimensions responded similarly to certain ecological determinants. Nevertheless, some authors observed that they responded in opposite or unexpected ways (e.g., de Solan et al., 2018; Rosas-Espinoza et al., 2022), which could be due to the specific functional traits selected by the authors. Each functional trait usually explain an species' specific response to a particular environmental condition (e.g., Ribeiro et al., 2017; García-Llamas et al., 2019). For example, amphibians reproductive traits (e.g., reproductive mode, development time) may explain species responses to pond characteristics (e.g., Lemckert & Mahony, 2010; Ribeiro et al., 2017; Baffa-Trasci et al., 2020; Atkinson et al., 2021), while habits (e.g., terrestrial, arboreal) and body size may explain responses to vegetation characteristics and land use change (e.g., Ribeiro et al., 2017). When calculating functional diversity metrics using a combination of traits, the resulting patterns heavily rely on the selection of these traits (Tsianou & Kallimanis, 2016, 2017), and a careful consideration of which traits are pertinent to the specific ecological determinant under investigation can elucidate observed patterns more effectively. Therefore, it is crucial to first explore how each trait (or combination of traits) responds to each determinant, as this knowledge essentially guides the selection of appropriate traits for a specific ecological determinant, enhancing the accuracy and relevance of subsequent analyses.

On the other hand, most studies tended to measure similar morphological, behavioral and life history traits (e.g., body size, reproductive mode, diet, habits) at different scales and contexts, which may help us discern which traits may be relevant at a particular scale. Nevertheless, this may also limit our understanding by choosing traits that may be not important at a particular scale or that are proxies of relevant functional traits, which may contribute to the opposite or unexpected patterns observed in some studies. For example, physiological traits such as thermal tolerances may be relevant at the local, landscape and regional scale where macro- and micro-climate is an important determinant, whereas defensive behaviors may be relevant particularly at the local scale, where biotic interactions are prevalent. Measuring other functional traits, such as body temperature, coloration or defensive behavior (Pianka et al., 2017), which seems to be rarely measured in most studies, may help further our understanding of species responses to environmental gradients at different scales.

FINAL CONCLUSIONS

Our perspective described the intricate interplay of ecological determinants shaping amphibian and reptile diversity across various spatial scales, as well as some important knowledge gaps that would be interesting to explore. We advocate for multi-scale studies to decipher the complex dynamics underlying species diversity, identifying the scale at which ecological determinants exert the strongest influence. Additionally, the careful selection of functional traits is crucial, with traditional traits being complemented by lesser-explored ones, like thermal tolerances and defensive behaviors, which may be more relevant under specific conditions. Additionally, and probably more innovative, would be to incorporate analyses of species movements and population dynamics, as well as stochastic processes, which can also explain part of the patterns observed at the community level (e.g., Martins et al., 2015; Vásquez-Restrepo et al., 2022). Addressing these gaps and adopting a comprehensive, multi-scale and multi-disciplinary approach, will not only deepen our understanding of species responses to environmental change but also inform effective conservation strategies in the face of ongoing anthropic impacts and climate change.

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APPENDIX

Appendix 1. Methods

We compiled scientific papers from Web of Science and Scopus database on June 2nd 2022, and updated again in July 5th 2023 for additional papers. We used the following search terms: (amphibian* OR reptile* OR herpetofauna* OR anuran* OR caecilian* OR salamander* OR lizard* OR snake* OR crocodile* OR turtle*) AND ("community structure" OR diversity OR assemblage* OR "functional group*" OR "functional trait*" OR trait*) AND (environmental* OR climatic* OR abiotic* OR biotic* OR anthropic* OR ecological) AND (determinant* OR driver* OR factor* OR variable* OR effect*) AND ("across scale*" OR "multiple scale*" OR "regional scale*" OR "landscape scale*" OR "local scale*" OR "scaling issue*" OR scale*). We also used the following algorithm in order to find additional articles related to biotic interactions: (amphibian* OR reptile* OR herpetofauna* OR anuran* OR caecilian* OR salamander* OR lizard* OR snake* OR crocodile* OR turtle*) AND ("assembly rules" OR "checkerbording" OR "niche overlap" OR "co-ocurrence*") AND ("community structure" OR diversity OR assemblage* OR "functional group*" OR "functional trait*" OR trait*). The above search terms were searched in 'Title', 'Abstract' and 'Keywords' fields. We tried to use a great variety of search terms combinations in order to find most scientific manuscripts that analyzed amphibian and reptile taxonomic and functional diversity patterns at regional, landscape and local scales, and their relationships with different ecological drivers.

We only considered studies that used the concept of scale explicitly in their analyses and worked at local, landscape or regional scales (although some not mentioning it explicitly or performed at global or continental scales are mentioned for further examples or explanations). Furthermore, only studies that dealt with amphibians or reptiles communities, but not individual species, were taken into account (although some examples of studies dealing with individual species are mentioned particularly for biotic interactions). We also only considered studies dealing with taxonomic and functional diversity, not phylogenetic diversity, as we were particularly interested in how different traits or functional groups were affected by different ecological determinants. Finally, only studies that measured and correlated ecological drivers (e.g., biotic, abiotic or anthropic determinants) with the structure of amphibian and reptile communities were taken into account (studies that only described amphibian and reptile diversity in a particular location were not taking into account).

The initial search resulted in 1,034 studies from Web of Science and 770 from Scopus, but only 207 were ultimately considered relevant and cited in this perspective, since this initial search revealed numerous studies that: 1) were unrelated to the topic (e.g., assessments of species extinction risk), 2) addressed phylogenetic diversity, 3) focused on other taxonomic groups (e.g., plants, parasites of amphibians and reptiles), 4) examined the relationship of an ecological determinant with a single species, 5) described amphibian and reptile diversity in a particular location without measuring any ecological determinant, or 6) did not mentioned the scale of analysis explicitly. Therefore, those studies were not considered.

Appendix 2. Bibliographic references used for the examination of the major ecological determinants affecting amphibian and reptile diversity patterns at regional, landscape, and local scales. For each reference, we described at which spatial scale the study was performed, which taxonomic group was evaluated (amphibians, reptiles or both), the diversity dimension studied, the functional traits (in case the author performed any functional diversity analysis) and the functional diversity measure or index used, and the main determinants evaluated according to the classification in Table 1. For reference codes see the footnote at the end.

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
1	Continental and Regional	Amphibians (Salamanders)	Taxonomic and functional	Size guild	Functional guilds	Biotic interactions (competition)
2	Local	Amphibians	None. Species occupancy	-	-	Biotic interactions (facilitation)
3	Landscape and Local	Amphibians	Taxonomic	-	-	Landscape configuration and semiaquatic environment's micro-habitat characteristics
4	Landscape	Amphibians	Taxonomic	-	-	Landscape configuration
5	Landscape	Amphibians	Taxonomic and functional	Body size, micro-habitat preference, reproduction type	Rao's quadratic entropy, functional dissimilarity and nestedness	Landscape configuration
6	Landscape	Amphibians	Taxonomic and functional	Micro-habitat preference	Mean values, functional dissimilarity	Landscape configuration
7	Regional	Reptiles (Lizards)	Taxonomic	-	-	Biotic interactions (competition)
8	Global and Regional	Amphibians	Taxonomic	-	-	Macro-climatic conditions, topographic heterogeneity
9	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, topographic heterogeneity, water-energy inputs
10	Landscape	Amphibians and Reptiles	Taxonomic	-	-	Landscape configuration
11	Local	Amphibians	Taxonomic and functional	Body size, development time, reproduction season	Mean values	Semiaquatic environment's micro-habitat characteristics
12	Landscape and Local	Amphibians	Taxonomic and functional	Reproductive mode and phenology, ecomorphological guild, micro-habitat preference, body size	Functional diversity index	Semiaquatic environment's micro-habitat characteristics, landscape composition and configuration
13	Local	Reptiles (Lizards)	Taxonomic and functional	Diet breadth	Mean values	Biotic interactions

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
14	Regional	Reptiles	Taxonomic and functional	Diurnal activity, reproductive mode, body size, annual fecundity, age at sexual maturity, habits, perturbance resistance, diet	Functional richness, dispersion and evenness	Macro-climatic conditions, land use change
15	Regional	Amphibians and Reptiles	Taxonomic	-	-	Landscape compositional heterogeneity, water-energy inputs, evolutionary dynamics
16	Local	Reptiles	Taxonomic and phylogenetic (diversification rates)	-	-	Terrestrial environment's micro-habitat characteristics
17	Landscape and Local	Amphibians	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, micro-climatic conditions, landscape configuration
18	Landscape	Amphibians and Reptiles	Taxonomic	-	-	Landscape configuration
19	Regional and Local	Amphibians	Taxonomic	-	-	Water-energy inputs, landscape compositional heterogeneity, regional pools
20	Landscape	Reptiles	Taxonomic and functional	Diet, foraging behavior, micro-habitat preference, activity pattern, body size, biomass	Functional richness, dispersion and evenness	Land use change
21	Local	Amphibians	Functional	Number of calling males per time period	Temporal acoustic niche breadth and overlap	Micro-climatic conditions
22	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, landscape composition and configuration, biotic interactions (competition)
23	Landscape and Local	Amphibians	Taxonomic	-	-	Terrestrial and Semiaquatic environment's micro-habitat characteristics, landscape configuration
24	Landscape and Local	Amphibians	Taxonomic	-	-	Land use change

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
25	Local	General theory for various taxonomic groups	Taxonomic	-	-	Biotic interactions (facilitation)
26	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, landscape configuration
27	Landscape and Local	Reptiles (Snakes)	Taxonomic	-	-	Macro-climatic conditions, landscape configuration, terrestrial environment's micro-habitat characteristics
28	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, landscape configuration
29	Regional and Landscape	Amphibians and Reptiles	Taxonomic	-	-	Land use change
30	Local	Amphibians	Taxonomic and functional	Body size, call frequency, breeding habitat	Mean pairwise phenotypic distance	Semiaquatic and Terrestrial environment's micro-habitat characteristics
31	Regional	Amphibians	Taxonomic and functional	Body size, micro-habitat preference, reproduction type, presence of larva, spawn site, site of larva development, parental care	Rao's quadratic entropy	Macro-climatic conditions
32	Local	General theory for various taxonomic groups	Taxonomic	-	-	Biotic interactions
33	Landscape	Amphibians	Taxonomic	-	-	Landscape compositional heterogeneity, landscape configuration
34	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Land use change
35	Landscape and Local	Amphibians	Taxonomic	-	-	Landscape configuration, semiaquatic environment's micro-habitat characteristics, biotic interactions (facilitation)
36	Landscape	Amphibians	Taxonomic	-	-	Land use change, landscape configuration

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
37	Landscape and Local	Amphibians	Taxonomic	-	-	Landscape configuration, semiaquatic environment's micro-habitat characteristics
38	Local	Amphibians	Taxonomic and functional	Reproductive mode	Functional groups	Micro-climatic conditions
39	Regional and Local	Amphibians	Taxonomic	-	-	Geographical distance, micro-climatic conditions, semiaquatic and terrestrial environment's micro-habitat characteristics
40	Regional and Local	Reptiles	Taxonomic and functional	Body size, diet, daily activity pattern, yearly activity pattern, locomotion type, micro-habitat preference, clutch size, age at sexual maturity, reproduction mode	Pairwise functional distances	Landscape composition and configuration
41	Landscape	Amphibians	Taxonomic	-	-	Landscape configuration, semiaquatic environment's micro-habitat characteristics
42	Regional and Local	Amphibians	Taxonomic, functional and phylogenetic	Micro-habitat preference, calling site, breeding seasonality, egg deposition site and type, tadpole type, body size, head width, hind-limb length, hand and foot webbing, terminal disks	Functional richness	Land use change
43	Regional	Reptiles	Taxonomic	-	-	Macro-climatic conditions, land use change
44	Regional and Local	Amphibians	Taxonomic	-	-	Historical barriers, terrestrial environment's micro-habitat characteristics
45	Local	Reptiles	Taxonomic	-	-	Small perturbations (fire regimes), terrestrial environment's micro-habitat characteristics
46	Local	Reptiles (Snakes)	Functional	Diet	Trophic niche overlap	Terrestrial environment's micro-habitat characteristics

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
47	Local	Reptiles (Lizards)	Taxonomic	-	-	Small perturbations (fire regimes), terrestrial environment's micro-habitat characteristics
48	Local	Reptiles	Taxonomic	-	-	Small perturbations (wood extraction), terrestrial environment's micro-habitat characteristics
49	Landscape	General theory for various taxonomic groups	Taxonomic	-	-	Landscape configuration
50	Landscape	Amphibians	Taxonomic	-	-	Landscape composition and configuration
51	Regional	Amphibians	Taxonomic and functional	Predominant lifestyle, reproductive strategy	Functional groups	Macro-climatic conditions
52	Regional and landscape	Amphibians and Reptiles	Taxonomic	-	-	Landscape compositional heterogeneity
53	Regional	Amphibians and Reptiles	Taxonomic and functional	Feeding guild, habitat use type, daily activity	Functional diversity index, functional redundancy	Macro-climatic conditions, topographic heterogeneity, land use change, water-energy inputs, landscape compositional heterogeneity
54	Regional	Amphibians	Taxonomic and phylogenetic (diversification rates)	-	-	Macro-climatic conditions, topographic heterogeneity, evolutionary dynamics
55	Global and Regional	Amphibians	Taxonomic and phylogenetic (diversification rates)	-	-	Topographic heterogeneity
56	Local	Reptiles (Lizards)	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics
57	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Land use change
58	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, topographic heterogeneity, land use change

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
59	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Landscape composition heterogeneity, landscape configuration
60	Regional and Landscape	Reptiles (Lizards)	Taxonomic, functional and phylogenetic	Body size, clutch size, sexual dimorphism, foraging mode, preferred microhabitat, activity period, reproductive mode	Pairwise functional distances	Historical barriers, micro-climatic conditions, terrestrial environment's micro-habitat characteristics
61	Regional and Local	Amphibians and Reptiles	Taxonomic	-	-	Regional pools
62	Regional, Landscape and Local	Amphibians (Salamanders)	Taxonomic	-	-	Macro-climatic conditions, geographical distance, landscape configuration, terrestrial environment's micro-habitat characteristics, elevation, slope
63	Regional and Local	Amphibians	Taxonomic	-	-	Geographical distance, terrestrial and semiaquatic environment's micro-habitat characteristics, slope
64	Global	Amphibians	Taxonomic	-	-	Historical and actual macro-climatic conditions, water-energy inputs
65	Landscape and Local	Amphibians	Taxonomic	-	-	Land use change
66	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, biotic interactions (predation), landscape configuration
67	Landscape and Local	Amphibians	Taxonomic	-	-	Land use change, landscape configuration
68	Landscape and Local	Amphibians	Taxonomic	-	-	Landscape configuration, semiaquatic environment's micro-habitat characteristics, biotic interactions (predation)

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
69	Regional	Reptiles (Lizards)	Taxonomic and functional	Body size, body shape, three-dimensional landmark coordinates from the head, lamella number, sexual size dimorphism	Mean values	Historical barriers, macro-habitat type
70	Regional and Local	General theory for various taxonomic groups	Taxonomic	-	-	Regional pools
71	Global and Regional	Amphibians and Reptiles	Taxonomic	-	-	Water-energy inputs
72	Regional	Amphibians and Reptiles	Taxonomic	-	-	Historical and actual macro-climatic conditions, land use change, macro-habitat type, geological processes
73	Local	Amphibians and Reptiles	Taxonomic	-	-	Land use change, terrestrial environment's micro-habitat characteristics
74	Landscape and Local	Amphibians	Taxonomic, functional and phylogenetic	Body size, toe webbing, mouth width, leg length, dorsum skin thickness/type, respiration type, fecundation type, male reproductive display for female response, male reproductive display site, fecundation site, egg laying site, parental care of clutches, daily activity, habitat during nonbreeding season, number of habitats used in nonbreeding season	Functional groups	Micro-climatic conditions, terrestrial environment's micro-habitat characteristics, land use change
75	Regional and Local	General theory for various taxonomic groups	Taxonomic	-	-	Biotic interactions
76	Regional and Local	Amphibians and Reptiles	Taxonomic	-	-	Regional pools
77	Landscape and Local	Amphibians	Taxonomic	-	-	Macro-climatic conditions, landscape configuration, land use change, terrestrial environment's micro-habitat characteristics

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
78	Landscape and Local	Amphibians	Taxonomic and functional	Diet, biomass	Trophic niche breadth	Land use change, macro-habitat type
79	Landscape and Local	Amphibians and Reptiles	Taxonomic and functional	Micro-habitat preference	Spatial niche breadth and overlap	Land use change, macro-habitat type
80	Local	Reptiles (Lizards)	Taxonomic and functional	Micro-habitat preference, body temperature, diet	Mean values	Biotic interactions (competition)
81	Landscape and Local	Amphibians	Taxonomic	-	-	Terrestrial and Semiaquatic environment's micro-habitat characteristics, landscape configuration
82	Regional	Reptiles (Lizards)	Taxonomic	-	-	Macro-climatic conditions, land use change, macro-habitat type
83	Regional and Local	Amphibians	Taxonomic and functional	Reproductive mode, clutch size	Functional groups	Macro-climatic conditions, land use change
84	Regional	Reptiles (Lizards)	Taxonomic	-	-	Macro-climatic conditions, topographic heterogeneity, water-energy inputs, geological processes
85	Continental and Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, land use change, geographical distance
86	Regional	Amphibians (Salamanders)	Taxonomic	-	-	Macro-climatic conditions, evolutionary dynamics
87	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, biotic interactions (predation), landscape configuration, elevation, slope
88	Local	Amphibians and Reptiles	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, land use change, macro-habitat type

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
89	Local	Reptiles (Lizards)	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, elevation, land use change, macro-habitat type
90	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, terrestrial environment's micro-habitat characteristics, land use change, macro-habitat type, small perturbations (grazing)
91	Regional and Local	Reptiles (Lizards)	Taxonomic and functional	Snout-vent length, forelimb length, hindlimb length, pectoral girdle width, pelvic girdle width, toe-pad width, head depth, jaw length, jaw width	Mean values	Historical barriers, macro-habitat type
92	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs, elevation
93	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, landscape configuration, biotic interactions (predation)
94	Landscape and Local	Reptiles (Lizards)	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, landscape configuration
95	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, landscape composition and configuration
96	Regional	Reptiles (Lizards)	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs, topographic heterogeneity
97	Regional and Landscape	Amphibians	Taxonomic	-	-	Macro-climatic conditions, landscape configuration, land use change

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
98	Landscape	General theory for various taxonomic groups	Taxonomic	-	-	Landscape configuration
99	Regional	Amphibians and Reptiles	Taxonomic, functional and phylogenetic	Trophic behaviour, microhabitat preference, body size, daily activity, reproduction, longevity, displacement mode	Functional diversity index	Regional pools, macro-climatic conditions, land use change, macro-habitat type
100	Regional	Reptiles (Lizards)	Taxonomic	-	-	Island's area
101	Local	Reptiles (Lizards)	Functional	Diet	Trophic niche segregation	Life history traits
102	Regional	Reptiles (Lizards)	Taxonomic and functional	Body size and shape, hindlimb length, tail length, color, number of subdigital lamellae	Functional groups	Historical barriers
103	Regional and Local	Reptiles (Lizards)	Taxonomic and functional	Diet, body size, micro-habitat preference	Mean values	Biotic interactions (competition)
104	Regional	Reptiles (Snakes)	Functional	Diet, habitat type	Spatial and trophic niche partitioning	Biotic interactions (competition)
105	Regional	Reptiles (Turtles)	Taxonomic	-	-	Biotic interactions (competition)
106	Landscape and Local	Reptiles	Functional	Diet	Food niche overlap	Land use change
107	Regional	Reptiles (Lizards)	Taxonomic and functional	Diet, habitat type	Mean values	Biotic interactions (competition)
108	Continental and Local	Reptiles (Turtles)	Taxonomic	-	-	Biotic interactions (competition)
109	Landscape and Local	Amphibians (Salamanders)	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, micro-climatic conditions, land use change, landscape configuration, small perturbations (wood extraction)
110	Regional and Local	Reptiles (Lizards)	Taxonomic	-	-	Historical barriers, landscape configuration, terrestrial environment's micro-habitat characteristics
111	Regional and Landscape	Amphibians	Taxonomic	-	-	Land use change, landscape configuration

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
112	Regional and Local	Amphibians	Taxonomic and phylogenetic	-	-	Evolutionary dynamics, stochastic processes
113	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Land use change, landscape configuration
114	Regional	Reptiles	Taxonomic	-	-	Region's area, topographic heterogeneity, macro-climatic conditions, water-energy inputs
115	Local	General theory for various taxonomic groups	None. Population dynamics	-	-	Stochastic processes
116	Landscape and Local	Amphibians and Reptiles	Taxonomic and functional	Snout-vent length, general habitat stratum, oviposition habitat, average number of offspring	Community-weighted mean	Land use change, landscape configuration, terrestrial environment's micro-habitat characteristics
117	Landscape and Local	Reptiles	Taxonomic	-	-	Land use change, landscape configuration, slope, elevation, aspect, terrestrial environment's micro-habitat characteristics
118	Local	Reptiles	Taxonomic	-	-	Land use change, macro-habitat type, small perturbations (fire regime)
119	Regional	Amphibians and Reptiles	Taxonomic and species distributions	-	-	Macro-climatic conditions, topographic heterogeneity, water-energy inputs, macro-habitat type, distance to hydrological networks
120	Landscape and Local	Reptiles	Taxonomic and functional	Micro-habitat preference	Functional groups	Small perturbations (grazing), terrestrial environment's micro-habitat characteristics
121	Global and Regional	Amphibians and Reptiles	Taxonomic and functional	Thermal strategy, body mass, trophic level	Functional groups	Land use change
122	Global and Regional	Amphibians and Reptiles	Taxonomic	-	-	Land use change
123	Global, Regional and Local	Amphibians and Reptiles	Taxonomic	-	-	Land use change

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
124	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, land use change
125	Landscape and Local	Amphibians	Taxonomic	-	-	Macro-climatic conditions, land use change, landscape configuration, terrestrial environment's micro-habitat characteristics
126	Local	Amphibians	Functional	Vocalization duration, structure and frequency	Spatial and temporal acoustic niche breadth and overlap	None
127	Continental and Regional	Amphibians	Taxonomic and functional	body size, primary habitat type, fertilization type, reproductive cycle, reproductive type, spawn site, presence/absence of larvae, site of development of larvae, presence/absence of parental care	Functional Hill's numbers	Water-energy inputs, macro-climatic conditions, aridity levels
128	Landscape and Local	Reptiles (Lizards)	Taxonomic, functional and phylogenetic	Body length, thermoregulation mode, type of habitat used, range of prey size	Rao's quadratic entropy, community-weighted mean, functional uniqueness	Landscape configuration
129	Local	Amphibians	Taxonomic	-	-	Land use change, small perturbations (wood extraction), terrestrial environment's micro-habitat characteristics
130	Regional and Local	Reptiles (Lizards)	Taxonomic	-	-	Macro-habitat type, evolutionary dynamics
131	Regional and Local	Reptiles (Lizards)	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics
132	Regional	Reptiles (Lizards)	Taxonomic and species distributions	-	-	Macro-habitat type
133	Local	Reptiles (Lizards)	Taxonomic and Functional	Diet, micro-habitat preference, activity pattern	Temporal, spatial and trophic niche partitioning	Biotic interactions (competition)
134	Landscape and Local	Amphibians (Salamanders)	None. Species occupancy	-	-	Semiaquatic environment's micro-habitat characteristics, landscape configuration, biotic interactions (predation)

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
135	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, landscape configuration, land use change
136	Landscape and Local	Amphibians	Taxonomic and functional	Body size, micro-habitat preference, reproductive mode	Functional guilds	Terrestrial environment's micro-habitat characteristics, landscape configuration
137	Regional	Amphibians	Taxonomic	-	-	Historical and actual macro-climatic conditions
138	Local	Reptiles (Lizards)	Taxonomic	-	-	Biotic interactions (facilitation)
139	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic and terrestrial environment's micro-habitat characteristics, landscape configuration
140	Global	Reptiles (Snakes)	Taxonomic	-	-	Evolutionary dynamics
141	Global and Regional	Reptiles (Snakes)	Taxonomic and phylogenetic	-	-	Macro-climatic conditions, water-energy inputs, island's area and isolation
142	Regional	Amphibians	Taxonomic and phylogenetic	-	-	Macro-climatic conditions, water-energy inputs, evolutionary dynamics
143	Global and Regional	Amphibians	Taxonomic and phylogenetic	-	-	Evolutionary dynamics
144	Regional and Local	Amphibians and Reptiles	Taxonomic	-	-	Water-energy inputs, topographic heterogeneity, plant richness
145	Global and Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs, topographic heterogeneity
146	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs, topographic heterogeneity
147	Regional and Local	Reptiles (Lizards)	Functional	Body size	Community-weighted mean	Macro-habitat type, biotic interactions (competition)

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
148	Regional and Local	Reptiles	Taxonomic	-	-	Regional pools
149	Local	Reptiles (Snakes)	None. Species occupancy	-	-	Terrestrial environment's micro-habitat characteristics
150	Landscape	Amphibians	Taxonomic	-	-	Land use change, landscape configuration
151	Global and Regional	Amphibians and Reptiles	Taxonomic	-	-	Historical and actual macro-climatic conditions, topographic heterogeneity, water-energy inputs, island's isolation
152	Landscape and Local	Amphibians	Taxonomic, functional and phylogenetic	Activity pattern, micro-habitat preference, habitat type, fossorial behavior, adult snout-vent length, breeding site, breeding strategy, clutch size, parental care, breeding season, breeding pattern, geographic range size	Rao's quadratic entropy, community-weighted mean	Terrestrial and Semiaquatic environment's micro-habitat characteristics, landscape configuration
153	Regional	Reptiles	Taxonomic	-	-	Macro-climatic conditions, topographic heterogeneity, land use change
154	Landscape and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, landscape configuration, biotic interactions (predation)
155	Local	Amphibians	Functional	Micro-habitat used, body size, time to metamorphosis	Mean values	Biotic interaction (competition)
156	Regional	General theory for various taxonomic groups	Taxonomic	-	-	Historical barriers, evolutionary dynamics
157	Regional and Local	General theory for various taxonomic groups	Taxonomic	-	-	Historical barriers, evolutionary dynamics, semiaquatic and terrestrial environment's micro-habitat characteristics, biotic interactions

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
158	Regional	Amphibians and Reptiles	Taxonomic	-	-	Region's area, topographic heterogeneity, elevation
159	Regional	Amphibians	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs, elevation
160	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Land use change, macro-habitat type, small perturbations (fire regime), terrestrial environment's micro-habitat characteristics
161	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs, landscape compositional heterogeneity, topographic heterogeneity
162	Global and Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions
163	Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, biotic interactions (facilitation)
164	Landscape and Local	Amphibians	Taxonomic and functional	Reproductive mode, diet, period of activity, micro-habitat preference, body size, type of skin, dorsal pattern, toxicity	Functional richness, evenness and divergence	Land use change, terrestrial environment's micro-habitat characteristics, small perturbations (grazing)
165	Landscape and Local	Reptiles	Taxonomic	-	-	Macro-climatic conditions, terrestrial environment's micro-habitat characteristics, slope, land use change, small perturbations (grazing), landscape configuration
166	Regional	Amphibians and Reptiles	None. Multivariate relationships between traits	Body size, body temperature, cutaneous evaporative water loss	Mean values	Macro- and micro-climatic conditions, water-energy inputs

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
167	Global and Regional	Reptiles (Lizards)	None. Multivariate relationships between traits	Body size, skin colour, thermal tolerance limits, preferred body temperature, thermoregulatory capacity	Community-weighted mean	Macro-climatic conditions, species' thermal performance
168	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Landscape configuration, land use change, terrestrial environment's micro-habitat characteristics
169	Landscape	Reptiles (Lizards)	Taxonomic	-	-	Landscape configuration
170	Landscape and Local	Amphibians	Taxonomic and functional	Breeding period, habitat use, reproductive modes	Functional groups	Semiaquatic and terrestrial environment's micro-habitat characteristics, macro-climatic conditions, biotic interactions (predation)
171	Local	Reptiles	Taxonomic and functional	Micro-habitat preference, altitudinal range, diet, age of sexual maturity	Mean values	Small perturbations (fire regime), terrestrial environment's micro-habitat characteristics
172	Landscape and Local	Amphibians	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, landscape configuration
173	Landscape and Local	Amphibians	Functional	Snout-to-vent length, Mouth width, Head length, Head width, Head height, Forelimb length, Thigh length, Tarsus-and-foot length, Shank length, Inter-orbital width, Eye diameter, Inter-narial distance, Narial-to-mouth distance	Average and standard deviation of nearest neighbor distance, average distance to centroid	Land use change, macro-habitat type, biotic interactions (competition)
174	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, landscape configuration, land use change
175	Local	Reptiles	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, biotic interactions (competition)

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
176	Local	Amphibians	None. Species occupancy	-	-	Biotic interactions (facilitation)
177	Landscape and Local	Amphibians	Taxonomic and species occupancy	-	-	Semiaquatic environment's micro-habitat characteristics
178	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, topographic heterogeneity, hydrological networks characteristics, vegetation heterogeneity
179	Local	Amphibians	Functional	Length of larval period, mass at metamorphosis, growth rate	Mean values	Biotic interactions (predation)
180	Local	Reptiles (Snakes)	None. Species occupancy	-	-	Landscape configuration, biotic interactions (competition)
181	Regional	Reptiles (Lizards)	Taxonomic	-	-	Macro-climatic conditions, geographical distance
182	Landscape and Local	Amphibians	Taxonomic and species occupancy	-	-	Landscape configuration, small perturbations (pollution)
183	Landscape and Local	Amphibians	Taxonomic and functional	Vocalization duration, structure and frequency, body size	Mean values	Landscape compositional heterogeneity, terrestrial and semiaquatic environment's micro-habitat characteristics
184	Local	Reptiles (Lizards)	Taxonomic	-	-	Small perturbations (pollution), terrestrial environment's micro-habitat characteristics
185	Global and Regional	Reptiles (Lizards)	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs, topographic heterogeneity, evolutionary dynamics
186	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Land use change
187	Regional	Amphibians	Taxonomic	-	-	Macro-climatic conditions, topographic heterogeneity, land use change

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
188	Local	Amphibians and Reptiles	Taxonomic and functional	Snout–ventral length, mean clutch size, active stratum, reproductive strategy, locomotion, feeding style	Functional groups	Terrestrial environment's micro-habitat characteristics, land use change
189	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Macro- and micro-climatic conditions, terrestrial environment's micro-habitat characteristics, elevation, slope
190	Local	Reptiles	Taxonomic	-	-	Land use change, macro-habitat type
191	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Landscape configuration, landscape compositional heterogeneity
192	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs
193	Global	Reptiles (Lizards)	Functional	Activity time, diet, micro-habitat preference	Functional groups	None
194	Local	Amphibians	Taxonomic	-	-	Biotic interactions (competition), macro-habitat type
195	Local	Amphibians	Taxonomic	-	-	Micro-climatic conditions
196	Landscape and Local	Reptiles (Snakes)	Taxonomic and species occupancy	-	-	Macro-climatic conditions, landscape configuration, biotic interactions (competition)
197	Landscape and Local	Amphibians and Reptiles	Taxonomic	-	-	Terrestrial environment's micro-habitat characteristics, landscape configuration
198	Landscape and Local	Amphibians	Taxonomic and functional	Body mass, dessication resistance	Mean values	Land use change, landscape configuration
199	Landscape and Local	Amphibians (Salamanders)	Taxonomic and species occupancy	-	-	Terrestrial and Semiaquatic environment's micro-habitat characteristics, landscape configuration
200	Local	Amphibians	Taxonomic and species distributions	-	-	Semiaquatic environment's micro-habitat characteristics, biotic interactions (predation)

Reference number	Spatial scale	Taxonomic group	Diversity dimension studied	Functional traits used	Functional diversity measure or index	Ecological determinants evaluated
201	Regional	Amphibians and Reptiles	Taxonomic	-	-	Macro-climatic conditions, water-energy inputs
202	Global and Regional	Amphibians	Taxonomic	-	-	Evolutionary dynamics
203	Regional	Reptiles (Lizards)	Taxonomic	-	-	Macro-climatic conditions, evolutionary dynamics
204	Local	Reptiles (Lizards)	Functional	Diet	Trophic niche overlap	Biotic interactions (competition)
205	Landscape	General theory for various taxonomic groups	Taxonomic	-	-	Landscape configuration
206	Regional and Local	Amphibians	Taxonomic	-	-	Semiaquatic environment's micro-habitat characteristics, land use change
207	Regional	Amphibians	Taxonomic	-	-	Water-energy inputs

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