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MARTÍN DE JESÚS CERVANTES LÓPEZ

THE IMPORTANCE OF LANDSCAPE STRUCTURE AND LOCAL QUALITY FOR MAINTAINING AMPHIBIAN AND REPTILE DIVERSITY IN SHADED AGROFOREST SYSTEMS

ILHÉUS – BAHIA

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Tese de doutorado apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade da Universidade Estadual de Santa Cruz como requisito parcial para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.

Orientador: Dr. José Carlos Morante-Filho

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Sumário

Resumo

O avanço do desmatamento impulsionado pela agropecuária tem fragmentado paisagens tropicais e ameaçado grupos sensíveis como anfíbios e répteis. Frente a esse cenário, a conservação da herpetofauna deve considerar não apenas os remanescentes florestais, mas também o potencial ecológico de matrizes antrópicas, como os sistemas agroflorestais sombreados. A capacidade dessas agroflorestas em sustentar comunidades diversas depende de fatores ambientais em múltiplas escalas, ainda pouco compreendidos. Por isso, é essencial integrar preditores locais e de paisagem, bem como adotar uma abordagem de múltiplas facetas da biodiversidade — incluindo as dimensões taxonômica, funcional e filogenética — avaliando tanto a diversidade dentro dos sítios quanto a variação na composição entre eles. O objetivo geral desta tese foi avaliar como as características ambientais influenciam a capacidade dos sistemas agroflorestais de sombra de manter a diversidade de anfíbios e répteis em paisagens antropizados. Esta pesquisa foi desenvolvida em três capítulos. No primeiro capítulo, realizamos uma meta-análise global para avaliar se os sistemas agroflorestais podem manter a diversidade de anfíbios e répteis em comparação com as florestas nativas. Analisamos como os parâmetros comunitários (riqueza ou abundância) e os tipos de agrofloresta, com base nas características da vegetação descritas pelos estudos (simplificadas ou complexas), impactam a variação do tamanho de efeito geral. Também examinamos como a quantidade de cobertura florestal ao redor das agroflorestas afeta o tamanho do efeito. Por fim, calculamos o Índice de Sorensen com base em dados de incidência para investigar o grau de similaridade na composição de espécies de anfíbios e répteis entre os sistemas agroflorestais e as florestas nativas. Os resultados mostram que as agroflorestas abrigam menor riqueza e abundância de anfíbios em comparação com as florestas nativas, enquanto para os répteis, a abundância é maior e a riqueza similar. Agroflorestas complexas mantêm maior diversidade de répteis do que as simplificadas, as quais se assemelham mais às florestas nativas. A cobertura florestal ao redor teve efeito positivo na riqueza de répteis, indicando que agroflorestas em paisagens com alta cobertura florestal pode sustentar maior diversidade. Também descobrimos que metade das espécies de anfíbios e répteis observadas em agroflorestas são diferentes daquelas observadas em florestas nativas. No Capítulo 2, investigamos o impacto de fatores paisagísticos e locais sobre a riqueza e diversidade taxonômica, funcional e filogenética da herpetofauna em 30 agroflorestas de cacau localizadas em três regiões com diferentes contextos de uso do solo na Mata Atlântica. Para estimar a riqueza e diversidade de cada dimensão, utilizamos os números de Hill nas ordens 0 (riqueza) e 1 (diversidade). Os resultados deste estudo revelaram que os preditores ambientais mais influentes em ambos os táxons foram os relacionados à paisagem. Nos anfíbios, a cobertura de pastagens favoreceu a riqueza e diversidade taxonômica e filogenética, enquanto a densidade das bordas florestais e o número de fragmentos florestais afetaram negativamente a riqueza e diversidade funcional, respectivamente. Além disso, as regiões com maior cobertura de floresta nativa apresentaram uma menor riqueza funcional. Nos répteis, tanto a cobertura florestal quanto a densidade das bordas florestais tiveram um impacto positivo na riqueza de espécies e na diversidade filogenética. Por fim, algumas variáveis ambientais locais influenciaram as comunidades de répteis: a umidade relativa favoreceu a riqueza funcional e a diversidade, enquanto a temperatura teve um efeito negativo sobre a riqueza funcional. Finalmente, no capitulo 3, avaliamos os padrões de diversidade beta taxonômica, funcional e filogenética de anfíbios e répteis em 30 sistemas agroflorestais de cacau sombreado, distribuídos em três regiões com contextos contrastantes de uso da terra: alta cobertura de cacau (HAC), alta cobertura florestal (HFC) e baixa cobertura florestal (LFC). Analisamos como os preditores da paisagem (cobertura de floresta e pastagem), do ambiente local (abundância de árvores de sombra e cobertura do dossel) e espaciais (distância geográfica entre locais) influenciam a diversidade beta. A região HAC apresentou consistentemente os menores valores de diversidade beta entre os táxons e dimensões analisadas. Nessa região, a diversidade beta de anfíbios diminuiu com o aumento das diferenças na abundância de árvores de sombra e na cobertura do dossel, sugerindo um efeito homogeneizante da estrutura da vegetação. Por outro lado, na região HFC, a diversidade beta de anfíbios aumentou com a variação na abundância de árvores de sombra e na cobertura de pastagens, enquanto na região LFC, a distância geográfica foi o principal fator associado à composição das comunidades. Para os répteis, a diversidade beta em HAC foi explicada por diferenças na cobertura do dossel, ao passo que, em HFC, a cobertura florestal e a distância geográfica exerceram maior influência. Em LFC, apenas a diversidade beta filogenética respondeu aos preditores, diminuindo com o aumento da cobertura de gramíneas e aumentando com a distância entre os sítios. Esses padrões contrastantes reforçam a importância de uma abordagem multidimensional da diversidade beta entre diferentes contextos de paisagem, revelando como o contexto ambiental, filtros ecológicos e dispersão limitante interagem na estruturação das comunidades de anfíbios e répteis em cacaueiros sombreados. Esta tese reforça o papel estratégico dos sistemas agroflorestais na conservação da herpetofauna em paisagens transformadas. Em escala global, sistemas agroflorestais com vegetação nativa no entorno podem manter elevada diversidade de répteis e uma proporção significativa da fauna de anfíbios. No entanto a partir de uma abordagem em múltiplas escalas e dimensões da biodiversidade, demonstramos que a conservação de anfíbios e répteis depende tanto da complexidade estrutural das agroflorestas quanto do contexto paisagístico onde estão inseridas. Em escala local, as agroflorestas de cacau demonstraram que seu valor de conservação depende do contexto da paisagem: enquanto em paisagens dominadas por pastagens elas podem fornecer refúgio para anfíbios filogeneticamente diversos, em áreas mais úmidas e florestadas elas favorecem a riqueza e a diversidade filogenética de répteis. Por fim, nossos resultados demonstram que a diversidade beta taxonômica, funcional e filogenética de anfíbios e répteis em sistemas agroflorestais de cacau sombreado é influenciada pela distância geográfica, heterogeneidade ambiental e pelo contexto da paisagem. Esses efeitos variam conforme a região, o grupo taxonômico e a dimensão da diversidade analisada, evidenciando a importância de estratégias de conservação adaptadas ao contexto local. A promoção da complexidade estrutural nos sítios e a manutenção da conectividade e cobertura florestal no nível da paisagem são fundamentais para conservar a diversidade ecológica e evolutiva em paisagens tropicais modificadas.

Abstract

The advance of deforestation driven by agriculture and livestock has fragmented tropical landscapes and threatened sensitive groups such as amphibians and reptiles. In this scenario, the conservation of herpetofauna must consider not only forest remnants but also the ecological potential of human-modified matrices, such as shaded agroforestry systems. The ability of these agroforests to support diverse communities depends on environmental factors operating at multiple scales, which are still not fully understood. Therefore, it is essential to integrate local and landscape-level predictors, as well as adopt a multifaceted approach to biodiversity—incorporating taxonomic, functional, and phylogenetic dimensions—by evaluating both within-site diversity and variation in species composition among sites. The general objective of this dissertation was to assess how environmental characteristics influence the capacity of shaded agroforest systems to sustain amphibian and reptile diversity in human-modified landscapes. This research was developed across three chapters. In Chapter 1, we conducted a global meta-analysis to assess whether agroforestry systems can maintain amphibian and reptile diversity compared to native forests. We analyzed how community parameters (richness or abundance) and types of agroforestry, based on

vegetation characteristics described in the studies (simplified or complex), affect the variation in overall effect size. We also examined how the amount of surrounding forest cover influences the effect size. Finally, we calculated the Sorensen Index using incidence data to investigate the degree of species composition similarity between agroforests and native forests. The results show that agroforests support lower amphibian richness and abundance compared to native forests, whereas for reptiles, abundance is higher and richness is similar. Complex agroforests maintain higher reptile diversity than simplified ones, which are more similar to native forests. Surrounding forest cover had a positive effect on reptile richness, indicating that agroforests in landscapes with high forest cover can support greater diversity. We also found that half of the amphibian and reptile species observed in agroforests were different from those found in native forests. In Chapter 2, we investigated the impact of landscape and local factors on the taxonomic, functional, and phylogenetic richness and diversity of herpetofauna in 30 cocoa agroforests located in three regions with different land-use contexts in the Atlantic Forest. To estimate species richness and diversity for each dimension, we used Hill numbers of orders 0 (richness) and 1 (diversity). The results revealed that the most influential environmental predictors for both taxa were related to landscape. In amphibians, pasture cover favored taxonomic and phylogenetic richness and diversity, while forest edge density and the number of forest fragments negatively affected functional richness and diversity, respectively. Additionally, regions with greater native forest cover had lower functional richness. In reptiles, both forest cover and forest edge density had a positive impact on species richness and phylogenetic diversity. Some local environmental variables also influenced reptile communities: relative humidity favored functional richness and diversity, while temperature had a negative effect on functional richness. Finally, in Chapter 3, we evaluated patterns of taxonomic, functional, and phylogenetic beta diversity of amphibians and reptiles in 30 shaded cocoa agroforests across three regions with contrasting land-use contexts: high agroforest cover (HAC), high forest cover (HFC), and low forest cover (LFC). We analyzed how landscape (forest and pasture cover), local (shade tree abundance and canopy cover), and spatial (geographic distance among sites) predictors influence beta diversity. The region HAC consistently exhibited the lowest beta diversity across taxa and dimensions. In this region, amphibian beta diversity decreased with increasing differences in shade tree abundance and canopy cover, suggesting a homogenizing effect of vegetation structure. In contrast, in HFC, amphibian beta diversity increased with variation in shade tree abundance and pasture cover, while in LFC, geographic distance was

the main factor influencing community composition. For reptiles, beta diversity in HAC was explained by differences in canopy cover, whereas in HFC, forest cover and geographic distance had a greater influence. In LFC, only phylogenetic beta diversity responded to the predictors, decreasing with increasing grass cover and increasing with site-to-site distance. These contrasting patterns highlight the importance of a multidimensional approach to beta diversity across different landscape contexts, revealing how environmental context, ecological filters, and dispersal limitation interact in structuring amphibian and reptile communities in shaded cocoa systems. This dissertation reinforces the strategic role of agroforest systems in conserving herpetofauna in transformed landscapes. At a global scale, agroforestry systems surrounded by native vegetation can maintain high reptile diversity and a significant proportion of amphibian fauna. However, using a multi-scale and multi-dimensional approach, we demonstrate that the conservation of amphibians and reptiles depends on both the structural complexity of agroforests and the landscape context in which they are embedded. At the local scale, cocoa agroforests showed that their conservation value depends on the surrounding landscape: while in pasture-dominated landscapes they may provide refuge for phylogenetically diverse amphibians, in more humid and forested areas they support reptile richness and phylogenetic diversity. Lastly, our results demonstrate that the taxonomic, functional, and phylogenetic beta diversity of amphibians and reptiles in shaded cocoa agroforests is influenced by geographic distance, environmental heterogeneity, and landscape context. These effects vary depending on the region, taxonomic group, and diversity dimension considered, highlighting the need for conservation strategies tailored to local contexts. Promoting structural complexity at the site level and maintaining forest connectivity and cover at the landscape level are fundamental for conserving ecological and evolutionary diversity in modified tropical landscapes.

General Introduction

Agricultural, livestock, and forestry activities are the primary drivers of global forest loss, degradation, and fragmentation (Curtis et al. 2018; Bodo et al. 2021). These changes not only reduce essential resources and disrupt species interactions but also threaten wildlife populations and the ecological services they provide, accelerating species loss (Fahrig 2003; Pardini et al. 2018). As human populations grow and demand for agricultural products rises, deforestation is expected to intensify, emphasizing the urgent need for strategies that reconcile biodiversity conservation with agricultural production. In this context, two contrasting approaches seek to balance agricultural production and conservation: (1) land-sharing, which promotes wildlife-friendly farming within heterogeneous landscapes (Green et al. 2005), and (2) land-sparing, which concentrates agricultural production in specific areas to set aside larger regions for conservation (Green et al. 2005; Phalan 2018). Land-sharing enhances habitat connectivity and may support biodiversity by integrating agricultural landscapes with natural elements, fostering ecological services such as pollination and pest control. However, lower yields may increase pressure on surrounding natural ecosystems (Green et al., 2005; Phalan, 2018). Conversely, land-sparing can preserve extensive forest areas and safeguard species reliant on natural habitats (Hulme et al. 2013; Birch et al. 2024). Still, its dependence on high-intensity farming may result in excessive agrochemical use, increased water consumption, and deforestation, ultimately reducing habitat connectivity and threatening species survival (Perfecto and Vandermeer 2010).

Despite the dichotomy between these two approaches, some studies have suggested that a complementary approach may be the most effective way to conserve biodiversity in most human-modified landscapes, depending on the ecological and socio-economic context (Valente et al. 2022; Narayana et al. 2024). This combination may involve the designation of strictly protected large forest areas (land-sparing), while simultaneously enhancing the ecological quality of the surrounding matrix through sustainable land-use practices (land-sharing), achieving a balance between biodiversity conservation and human livelihoods (Kremen 2015; Arroyo-Rodríguez et al. 2020). In this context, a scientific framework for biodiversity conservation has been established, advocating for the enhancement of the ecological value of the surrounding matrix (Perfecto and Vandermeer 2008, 2010).

Recognizing the agroecological matrix as a potentially crucial component of biodiversity conservation represents a shift from traditional applications of the Theory of Island Biogeography, which was originally developed to explain species richness on oceanic islands. In these systems, the surrounding matrix (the ocean) acts as a complete barrier to the majority of terrestrial species, assuming habitat fragments effectively isolated units, analogous to true islands (Haila 2002). However, in fragmented landscapes, the matrix is often heterogeneous, with varying degrees of permeability for different species (Fletcher et al. 2024). For instance, studies on species diversity in agricultural matrices have shown that those with complex and forest-like vegetation structures can support higher species diversity compared to intensively deforested matrices, such as cattle pastures (Lara-Tufiño et al. 2019; Alvarez-Alvarez et al. 2022), or monocultures (Schroth and Harvey 2007; Mendenhall et al. 2014; Yahya et al. 2023). These findings highlight that certain agricultural matrices, particularly agroforests, can play critical roles as habitats (or complementary habitats) for a wide variety of plant and animal species (Pineda et al. 2005; Faria et al. 2007; Schroth and Harvey 2007; Perfecto and Vandermeer 2008).

Among shaded agroecosystems or agroforests, those integrating crops under a diverse canopy of native and exotic trees stand out for their potential to sustain biodiversity, as they create heterogeneous environments that support a variety of microhabitats and optimal microclimatic conditions (Moguel and Toledo 1999). This structural diversity enhances habitat quality by providing complementary and/or supplementary resources for a wide range of plant and animal species (Schroth and Harvey 2007; Deheuvels et al. 2014). Additionally, such vegetation complexity improves landscape permeability, facilitating species movement and migration (Ferreira et al. 2020; Valente et al. 2022; Manson et al. 2024). Research in tropical landscapes has shown that shaded agroforests, such as those used for coffee (*Coffea arabica* L.), vanilla (*Vanilla planifolia*), or cocoa (*Theobroma cacao* L.), can support significantly higher levels of biodiversity, with species composition often comparable to that of native forests (Schroth and Harvey 2007; Iverson et al. 2019; Hending et al. 2023). This has been found in numerous studies for different groups of organisms, including plants (Marconi and Armengot 2020; Zequeira-Larios et al. 2021), birds (Cabral et al. 2021; Jarrett et al. 2021), mammals (Caudill et al. 2014; Zárate et al. 2014; Silva et al. 2020), amphibians (Lara-Tufiño et al. 2019; Cervantes-López et al. 2022), reptiles (Ríos-Orjuela et al. 2024; Badillo-Saldaña et al. 2024), and invertebrates (Pywell et al. 2012; Ferreira et al. 2024).

Despite this, environmental factors at multiple spatial scales can shape the ability of shaded agroforests to sustain species diversity (Schroth and Harvey 2007; Cassano et al. 2014). Management intensity at a local scale and landscape structure at a larger scale may both drive heterogeneity, thus influencing matrix quality for biodiversity conservation

(Deheuvels et al. 2014; Hending et al. 2023). Matrix quality refers to the extent to which the matrix retains both a vertical and horizontal vegetation structure similar to that of the native vegetation, providing habitat complexity that supports diverse biological communities despite anthropogenic alterations (de Souza Leite et al. 2022; Fletcher et al. 2024). In cocoa plantations, management varies across three modalities with distinct canopy cover and vertical structure (Rice and Greenberg 2000): (1) Rustic cocoa, where cocoa grows under a native canopy (Fig. 1a); (2) commercial polyculture, which replaces part of the native canopy with economically valuable tree species (e.g., fruit and timber trees) (Fig. 1b); and (3) full-sun monoculture, reliant on agrochemicals for productivity and pest control (Fig. 1c). Along this gradient, cocoa matrices vary in their microclimatic conditions, influencing species diversity and community composition (Deheuvels et al. 2014; Jarrett et al. 2021; Bennett et al. 2022). For instance, cocoa agroforests with greater tree species richenss, a closed canopy, and higher structural complexity create conditions more similar to native forests, promoting higher species diversity and offering essential microhabitats for many organisms (Clough et al. 2009; Wanger et al. 2010; Cabral et al. 2021).

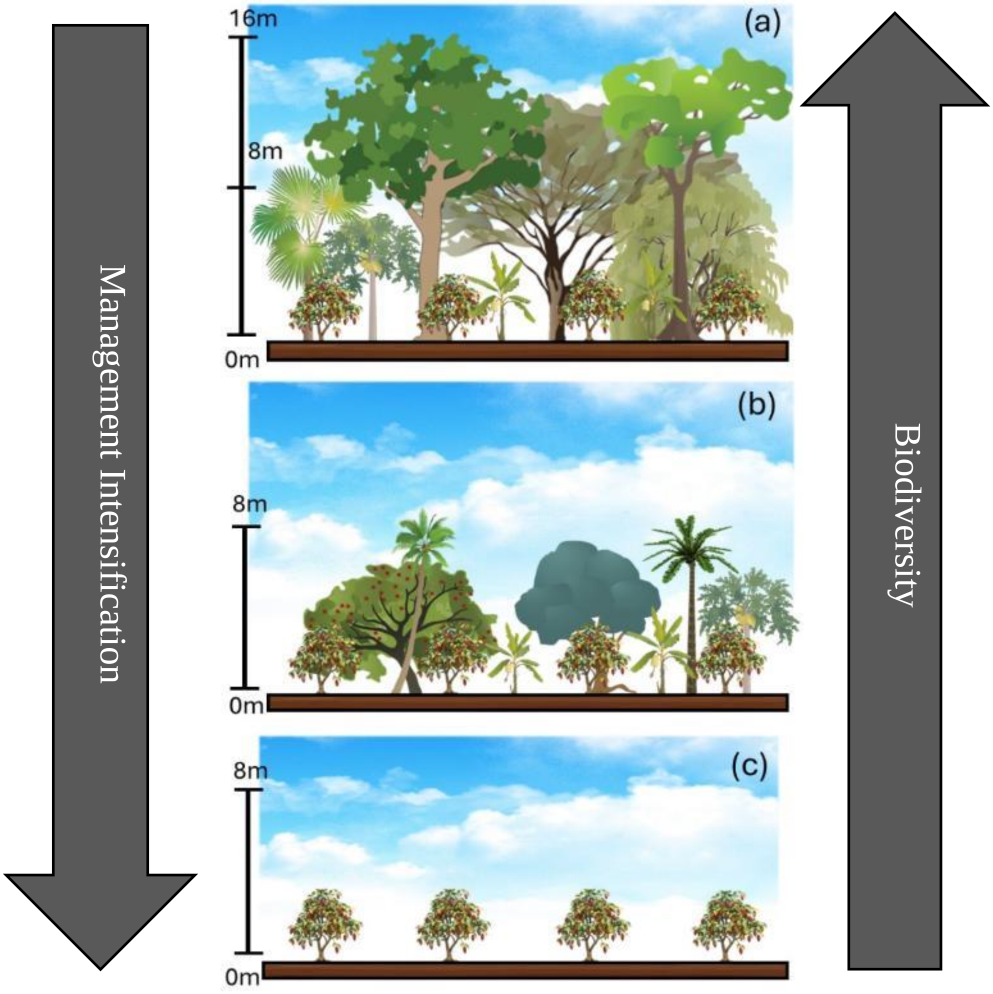
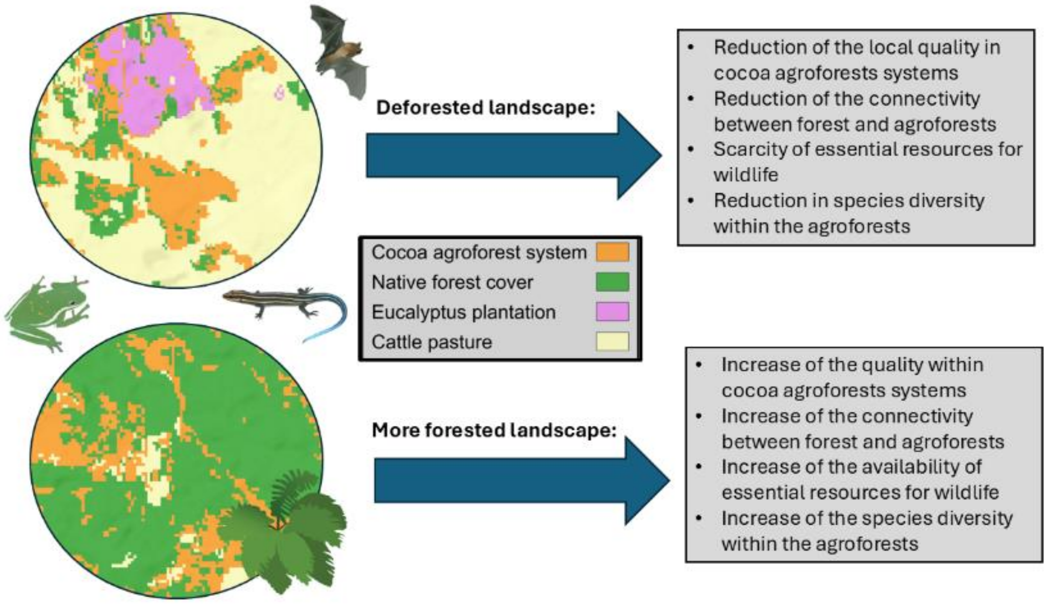


Figure 1. The management gradient of cocoa production. The management gradient of cocoa production. Along this gradient, increased management intensity leads to a progressive reduction in shade tree diversity and structural complexity. (a), giving way to systems dominated by some commercial species of lower height (b) and even to monocultures in full sun (c). In this context, as cocoa systems become simpler, they may lose resources and conditions necessary to maintain high species diversity. Figures modified from: Rice and Greenberg 2000 and Perfecto et al. 2019. Image sources: [*https://vecta.io/symbols*] and [*https://www.pngwing.com/pt*].

In addition to management intensity, landscape structure plays a crucial role in shaping the quality of agroforests as habitats for biodiversity (Weibull et al. 2002; Schroth and Harvey 2007). Studies in cocoa agroforest systems and native forest in Brazil have shown that regional forest cover influences species richness and community composition of animal and plant communities (Faria et al. 2007; Cabral et al. 2021; Ferreira et al. 2024, 2025). A higher proportion of forest cover in the landscape may enhance species movement and resource availability within agroforests, functioning as complementary or supplementary habitats for biodiversity (Alvarez-Alvarez et al. 2022; Bedoya-Durán et al. 2023) (Fig. 2). However, factors such as the extent of open areas and the characteristics of forest-agroforest edges can influence species dispersal and connectivity between forest patches and agroforest systems. While large open areas may restrict movement and weaken connectivity (Cabral et al., 2021) (Fig. 2), less abrupt transition zones between forests and agroforests can create heterogeneous abiotic conditions that enhance resource availability and facilitate species movement (Haggar et al. 2019). Yet, the creation of these heterogeneous transition zones may also expose species to human disturbances and facilitate the spread of generalist species (Fletcher et al. 2024). Despite these insights, further research is needed to better understand how landscape predictors influence biodiversity in agroforestry systems and their role in conservation.



- Reduction of the local quality in cocoa agroforests systems
- Reduction of the connectivity between forest and agroforests
- Scarcity of essential resources for wildlife
- Reduction in species diversity within the agroforests

- Increase of the quality within cocoa agroforests systems
- Increase of the connectivity between forest and agroforests
- Increase of the availability of essential resources for wildlife
- Increase of the species diversity within the agroforests

Figure 2. Landscape-scale structure modulates the local quality of the cocoa agroforestry systems to host high species diversity in deforested landscapes. This example in the south of Bahia state, Brazil, illustrates how landscape context (comparing a deforested landscape with a more forested one) influences the quality of the cocoa agroforestry systems as habitat for native biodiversity (Faria et al. 2007). In deforested landscapes, connectivity between forest fragments and agroforests is lower, essential resources for wildlife are scarcer, and species diversity within the agroforests decline. In contrast, more forested landscapes promote a higher quality of the agroforests, with greater connectivity, enhanced resource availability, and higher species diversity within cocoa agroforests. Image sources: [*https://vecta.io/symbols*].

Despite these insights, further research is needed to better understand how landscape or local factors influence biodiversity in agroforests and their role in conservation. Among the species negatively affected by landscape changes, amphibians and reptiles stand out due to their unique ecophysiological characteristics, which make them highly sensitive to environmental disturbances (Gibbons et al. 2000). Additionally, their specialized dietary and habitat requirements further exacerbate their vulnerability. Habitat loss and degradation, climate change, pollution, invasive species, illegal wildlife trade, and emerging diseases have all contributed to severe population declines of these animals (Cox et al. 2022; IUCN SSC Amphibian Specialist Group 2024). In particular, habitat loss and degradation not only restrict species movement but also limit their access to essential resources such as shelter, food, and suitable microclimatic conditions for survival and reproduction (Ficetola et al. 2015; Farooq et al. 2024). Additionally, these disturbances can increase the prevalence of infectious diseases, posing a significant threat to anurans (Becker et al. 2023). Currently, 41% of evaluated amphibian species (2,873 out of 8,009) and 21% of evaluated reptile species (1,847 out of 10,311) face extinction risks (IUCN 2024), highlighting the urgent need for targeted conservation strategies. The loss of these species could have cascading effects on ecosystems, as they play key roles as both predators and prey in food chains, in addition to contributing to crucial ecosystem functions, such as pest control, nutrient cycling, and the production of bioactive compounds with medicinal potential (Valencia-Aguilar et al. 2013; Cortés-Gómez et al. 2014; Zipkin et al. 2020). Given these global threats, understanding how local wildlife-friendly land uses, such as shaded cocoa agroforests, can mitigate some of the negative impacts on amphibians and reptiles is crucial for ensuring the persistence of these species in human-modified landscapes.

Several studies have shown that different matrices, such as cattle pastures or African oil palm plantations (*Elaeis guineensis*), are often unsuitable for forest-associated reptile and amphibian species (Mendenhall et al. 2014; Gallmetzer and Schulze 2015; Cruz-Elizalde et al. 2016). These results are consistent with those of a recent meta-analysis (López-Bedoya et al. 2022) that evaluated the impacts of various plantation types on the abundance and richness of amphibians and reptiles. This study revealed that pastures exert a negative impact on herpetofauna, while other types of matrices, such as certain types of tree plantations, although still affecting these species, may have comparatively milder effects depending on their structural complexity and management. However, it is important to note that some tree plantations, such as African oil palm, can have similarly negative impacts of herpetofauna communities as pastures (Gallmetzer and Schulze). Moreover, shade agroforests that have structural similarity to native forests, can provide suitable habitat for many amphibian and reptile species (Heinen 1992; Fulgence et al. 2022; Cervantes-López et al. 2022).

Notwithstanding the growing number of studies on herpetofauna, there is still no clear consensus on how these groups respond to shade agroforests, as findings remain variable and, in some cases, contradictory. While some studies report higher species richness, abundance, or diversity of herpetofauna in native forests compared to agroforests (Faria et al., 2007; Pineda and Halffter, 2004), others show different patterns (Cervantes-López et al., 2022; Whitfield et al., 2007), suggesting that these systems can also support herpetofaunal communities. These discrepancies highlight the need for synthesis studies, such as meta-analyses, to consolidate existing knowledge, clarify these patterns, identify knowledge gaps, and evaluate the role of agroforests systems in biodiversity conservation.

Studies suggest that different types of agroforests vary in their ability of sustaining forest-specialist species, thus being dominated by generalist species (Faria et al., 2007; Wanger et al., 2009; Whitfield et al., 2007). However, as in many other groups, environmental conditions at the local and landscape scales may influence the diversity and composition of amphibians and reptiles in agroforests (Faria et al. 2007; Wanger et al. 2009; Vega-Agavo et al. 2021). For example, it has been found that specific abiotic conditions and the availability of microhabitats, such as a dense leaf litter layer, trunks, and a closed canopy with emergent native trees, may favor biodiversity in cocoa and coffee agroforests (Pineda and Halffter 2004; Wanger et al. 2010; Brüning et al. 2018; Ríos-Orjuela et al. 2024). Also, although few studies have examined the influence of landscape structure on shaded agroforests, those that have suggest that forest cover plays a significant role in shaping herpetofaunal diversity and composition. For example, in southern Bahia, Brazil, Faria et al. (2007) observed that cocoa agroforests in landscapes with lower forest cover harbored different anuran and lizard communities than those in regions with higher forest cover. In a study in avocado agroforests in Mexico, the reduction of native forest cover at the landscape level, negatively affected specialist frogs and snakes, while generalist species, such as anurans, salamanders and lizards, increased in abundance and richness in more deforested landscapes (Vega-Agavo et al. 2021).

Most studies addressing the role of agroforests in maintaining herpetofaunal diversity have predominantly focused on taxonomic diversity metrics (Cervantes-López et al., 2022; Macip-Ríos and Muñoz-Alonso, 2008; Wanger et al., 2010). Relying solely on taxonomic diversity offers a limited perspective, as it overlooks functional traits and evolutionary histories that shape species’ responses to environmental change (Naeem et al. 2012; Ribeiro et al. 2017). Including functional and phylogenetic diversity provides deeper insights into ecosystem functioning and resilience, and is thus essential for assessing habitat quality in agroforests under anthropogenic pressures (López-Bedoya et al. 2022; Devictor et al. 2010). Considering these dimensions is key because they may show different responses to environmental changes at both local and landscape scales. For example, in amphibians, species with large body sizes, terrestrial habits, and aquatic-dependent reproduction are more sensitive to the loss of canopy cover and forest transformation (Pineda and Halffter 2004). In tropical snakes, forest cover reduction in the landscape diminishes species richness and functional diversity, with higher forest proportions and more patches promoting greater abundance. However, phylogenetic diversity is more closely linked to the composition of local habitats (Leal-Santos et al. 2024). In this sense, these dimensions could provide us with the opportunity to have a more complete understanding of how agroforests can sustain ecological processes, preserve species richness and maintain the long-term productivity and stability of these managed landscapes.

Beyond assessing how local environmental characteristics shape species diversity within shaded agroforests, it is also essential to understand whether environmental variation across sites influences species composition at broader spatial scales (Kessler et al. 2009; Roa-Fuentes et al. 2019). In this context, beta diversity—reflecting patterns of community dissimilarity—becomes a key metric for evaluating the ecological role of agroforests in biodiversity conservation, including amphibians and reptiles (Clough et al. 2009; Marconi and Armengot 2020). When analyzed alongside environmental and spatial gradients, beta diversity can offer insights into the processes driving biotic homogenization or differentiation (Olden 2006; Socolar et al. 2016), supporting broader efforts in conservation planning (Tscharntke et al. 2012). Both local factors, such as canopy density or microclimatic regulation (Palmeirim et al. 2017; Lourenço-de-Moraes et al. 2020), and landscape-level variables, like forest cover and habitat connectivity, significantly influence beta diversity patterns (Faria et al. 2007; Da Cunha Bitar et al. 2015). Importantly, previous studies have shown that landscape structure modulates these patterns, with the influence of environmental and spatial predictors varying considerably across regions with contrasting levels of forest cover (Arroyo-Rodríguez et al. 2013; Morante-Filho et al. 2016). Although few studies have addressed this issue for amphibians and reptiles, their high vulnerability to habitat changes highlights the need to explore how landscape heterogeneity shapes beta diversity across multiple spatial scales.

The southern region of Bahia, Brazil, offers a suitable setting to investigate the effects of habitat fragmentation and land-use change on species diversity and community composition, as it consists of highly fragmented landscapes with cocoa agroforests, native forest remnants, eucalyptus plantations, and cattle pastures. Cocoa agroforests in this region trace their origins back to the 19th century when many farmers began establishing cocoa plantations, gradually replacing other crops such as sugarcane (Lopes et al. 2011; MapBiomas 2023). Over time, farmers adopted shaded agroforest systems, traditionally known as “cabrucas”, as an alternative to monocultures, integrating cocoa cultivation with native tree species of the Atlantic Forest (Fig. 3) (Fernandes et al. 2019; Sambuichi et al. 2012). This transition to shaded agroforests has been fundamental for biodiversity conservation, improving connectivity between forest fragments and providing refuge for species endemic to the area (Cassano et al. 2009; Faria et al. 2007; Schroth et al. 2011). In addition, the presence of abundant and diverse shade trees in these agroforests enhances structural complexity and biomass, allowing them to sequester up to 59% of carbon, thus contributing to climate change mitigation (Scroth et al. 2015). Currently, it is estimated that there is an area of 6,562 km2 of shaded cocoa distributed in 83 municipalities in southern Bahia (Biomes Map 2023). However, these systems face persistent challenges, including market pressures (Sambuichi et al. 2012), diseases affecting production (Chiapetti 2014), climate change (Heming et al. 2022), and the removal of shade trees in favor full-sun monocultures (Schroth et al. 2015). These threats underscore the urgency of studying their role in the conservation of southern Bahia's biodiversity.

Figure 3. Cocoa agroforests in southern Bahia. This type of shaded agroforest consists of cocoa trees grown under a diverse canopy of native tree species, along with exotic trees and/or commercially valuable species.

The southern region of Bahia, home to extensive cocoa agroforests, is also situated within one of Brazil's most significant biomes: the Atlantic Forest. This biome, extending along Brazil's eastern coast into northern Argentina and eastern Paraguay, is one of the most biodiverse biomes globally. It harbors approximately 20,000 vascular plant species, with 8,000 being endemic, and nearly 2,700 vertebrate species, including 719 amphibians, 504 of which are endemic, and 517 reptiles, 126 of which are endemic to this biome (Figueiredo et al. 2021). However, this biome has suffered a significant loss of forest cover, with only 24% of its original area remaining (Amaral et al. 2025). As deforestation continues, understanding how high-quality matrices like cocoa agroforests support herpetofauna conservation in this human-modified region is vital. Without conservation efforts, many endemic amphibians and reptiles risk extinction.

The general objective of this thesis was to assess how environmental characteristics influence the ability of shaded agroforestry systems to maintain amphibian and reptile diversity in human-modified landscapes. To address this objective, we conducted three studies, each constituting a chapter of this thesis. In the first chapter, we performed a global meta-analysis to evaluate how agroforests support amphibian and reptile species richness and abundance compared to native forests. In the second chapter, we investigated the impact of landscape and local factors on the taxonomic, functional, and phylogenetic diversity of herpetofauna in 30 shaded cocoa agroforests across three regions in the Brazilian Atlantic Forest of southern Bahia. Finally, we explored patterns and predictors of beta diversity in amphibian and reptile communities, considering taxonomic, functional, and phylogenetic dimensions, across the same regions.

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Capítulo 1. A global meta-analysis on patterns of amphibian and reptile diversity in agroforestry systems

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A global meta-analysis on patterns of amphibian and reptile diversity in agroforestry systems

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Abstract

Global herpetofauna faces threats by habitat loss and degradation, with amphibian and reptile species maintenance in human-modified landscapes not only depending on forest remnants, but also on biodiversity-friendly matrices, such as agroforestry systems. Nevertheless, herpetological studies in agroforests are limited, hindering conservation decisions. To fill this gap, we conducted a global meta-analysis to assess the ability of agroforestry systems to maintain abundance and richness of amphibian and reptile species when compared to native forests. We analyze how community parameters (richness or abundance) and agroforest types based on the vegetation characteristics described by the studies (simplified or complex) impact the variation of overall effect size. We also used meta-regression models to examine how the amount of forest cover around agroforests affects the effect size. Finally, we calculated Sorensen's Index based on incidence data to investigate the degree of similarity in species composition of amphibians and reptiles between agroforestry systems and native forests. Our results showed that amphibian diversity in agroforests is lower than in native forests, regardless of the parameter and agroforestry type. For reptiles, agroforests showed higher abundance and similar species richness to forests. Simplified agroforestry systems support less reptile diversity than complex systems, which are more similar to forests. Interestingly, landscape forest amount modulates the ability of agroforests in maintain reptile richness. In fact, agroforests inserted in highly forested landscapes can harbor higher richness of reptiles than forests. We also found that half of the amphibian and reptile species observed in agroforests are different from those observed in native forests. Our findings highlights that agroforests cannot replace native forests because such systems harbor reduced abundance and species richness, especially amphibians, and a distinct species composition. However, when inserted in forested landscapes these agricultural systems can host rich reptile communities.

Thus, preserving native forests and restoring deforested regions are crucial for herpetofauna conservation in human-modified landscapes.

***Keywords**:* Abundance, Agricultural systems, Habitat loss, Herpetofauna, Species richness, Wildlife-friendly agriculture

Introduction

Land-use changes driven by agricultural activities lead to forest loss and degradation around the terrestrial biosphere (Curtis et al., 2018, Ellis et al., 2013, Ellis et al., 2010). This situation has converted natural landscapes into a series of forest remnants surrounded by distinct anthropogenic matrices (Melo et al., 2013) that negatively affect biodiversity (Newbold et al., 2015). In this context, different strategies have been developed to mitigate the impacts of habitat loss and fragmentation on species diversity (Arroyo-Rodríguez et al., 2020, Soley and Perfecto, 2021). In particular, several studies highlight the pivotal role that wildlife-friendly matrices, such as agroforestry systems, can presents for the protection of native species in human-modified landscapes (Perfecto and Vandermeer, 2008, Santos et al., 2021). Based on FAO (2020), agroforestry systems cover an extensive area of 45.432 Mha around the world, particularly distributed in Asia, Africa, and Americas (Raj et al., 2024). In fact, agroforestry systems exhibiting greater complexity in the vegetation structure can provides a variety of environmental conditions and micro-habitats necessary for the survival and reproduction of plant and animal assemblages (Altieri, 1999, Bhagwat et al., 2008, Niether et al., 2020, Rocha et al., 2019, Yashmita-Ulman et al., 2021). In these systems, crops are grown under the shade of native and exotic trees, creating an ecosystem that can contribute to the farm economy, as well as to favoring the maintenance of native species in a given region (Nair et al., 2021). Despite the growing number of studies evaluating the role of agroforestry systems in the conservation of many organisms, there is still scarce information about the contribution of these systems to the maintenance of amphibian and reptile species in human-modified landscapes (Cervantes-López et al., 2022, Palacios et al., 2013).

In particular, the use of distinct environments in human-modified landscapes by native species, including anthropic matrices, is a cutting-edge issue in Ecology (Chazdon et al., 2009, Perfecto and Vandermeer, 2010). The habitat amount hypothesis posits a positive correlation between the habitat quantity at the landscape scale and species diversity of focal patch. According to this hypothesis, landscapes with a greater habitat amount can offer more resources and connectivity, enabling species to colonize different areas within the landscape and, consequently, decreasing the risk of extinction (Fahrig, 2013). In this context, biodiversity-friendly matrices, such as agroforestry systems, can have a vital impact on aiding the migration of species across fragmented habitats, simultaneously offering resources to alleviate the decline in biodiversity (Perfecto and Vandermeer, 2008). In fact, biodiversity-friendly matrices can be used as supplementary or complementary habitat for a wide range of native species, thus contributing to increased regional diversity (Dunning et al., 1992, Tscharntke et al., 2012). The loss and modification of natural habitats pose one of the greatest threats to the decline of amphibian and reptile species worldwide. In disturbed habitats, there is a limitation in the availability of food resources and shelters (Bishop et al., 2012; Doherty et al., 2020). Additionally, many species of amphibians and reptiles present limited dispersal capacity and high specialization in the use of microhabitats; characteristics that make them highly vulnerable to environmental changes (Bishop et al., 2012; Gibbons et al., 2010; Todd et al., 2010). As a result, almost 41% of 8020 amphibians and 21% of 10,254 reptile species are included in some category of extinction threat according to the IUCN (IUCN., 2023). Thus, the conservation of amphibians and reptiles has been so urgent (Cox et al., 2022, Luedtke et al., 2023). Furthermore, as these vertebrates are part of the trophic chain, acting both as predators and prey (Cortés-Gomez et al., 2015; Valencia-Aguilar et al., 2013), the extinction or even the population decline of amphibians and reptiles can have severe impacts on the functioning of native habitats. In this context it is essential to understand how agricultural matrices, including agroforestry systems, can assist in the conservation and permanence of the herpetofauna, given the growing deforestation worldwide (FAO and UNEP, 2020).

Although the number of studies on amphibian and reptile assemblages in agroforestry systems is limited, some research has shown that these wildlife-friendly matrices can serve as temporary or supplementary habitat for species that inhabit fragmented landscapes (Cervantes-López et al., 2022, Faria et al., 2007, Fulgence et al., 2021, Heinen, 1992, Pineda et al., 2005, Wanger et al., 2010). For instance, shaded agroforest systems (such as coffee and cocoa) may support similar or higher amphibian and reptile richness and abundance than native forests in tropical regions (Cervantes-López et al., 2022, Heinen, 1992, Lara-Tufiño et al., 2019, Macip-Ríos and Muñoz, 2008, Orozco et al., 2016, Whitfield et al., 2007). This retention of high herpetofauna diversity in agroforestry systems may be due to the adequate environmental conditions and resources, such as the presence of a thick layer of leaf litter, temporary and/or permanent ponds, fallen branches and trunks, high density of shrubs and canopy cover (Cervantes-López et al., 2022, Coria et al., 2016, Deheuvels et al., 2014, Wanger et al., 2010, Wanger et al., 2009). However, the conservation value of agroforestry systems for native species depend on environmental features acting in different spatial scales, such as local vegetation complexity and amount of landscape forest cover (Faria et al., 2007, Rice and Greenberg, 2000). In fact, some studies indicated that local management intensity in agroforestry systems can negatively impact amphibian and reptile diversity via vegetation simplification and the subsequent loss of microhabitats, leading to changes in abundance, richness and species composition of both taxa (Blumgart et al., 2017, Fulgence et al., 2021, Macip-Ríos and Muñoz, 2008, Wurz et al., 2022). For example, the replacement of native tree species by exotic trees can lead to a decrease in habitat structure complexity and a decline in habitat quality (Rice and Greenberg, 2000), consequently impacting negatively native vertebrate species, including amphibians and reptiles. In addition, agroforests inserted in highly forested landscapes can harbor great species diversity given that the greater habitat amount and the lesser isolation between patches (Faria et al., 2007, Pardini et al., 2009, Vega-Agavo et al., 2021).

Furthermore, the responses of amphibians and reptiles to agroforestry systems are variable and, in some cases, appear to be contradictory (Palacios et al., 2013). For instance, some studies report higher abundance of herpetofaunal species in native forest than in agroforestry systems (Evans, 2019, Faria et al., 2007, Lieberman, 1986, Murrieta-Galindo et al., 2013, Pineda and Halffter, 2004), while other works present distinct findings (Cervantes-López et al., 2022, Evans, 2019, Heinen, 1992, Whitfield et al., 2007). These discrepancies in species diversity patterns between herpetological studies performed in agroforests highlight the urgent need to conduct systematic investigations that can be performed through a meta-analytic approach (López-Bedoya et al., 2022). Indeed, systematic reviews allow to synthesize the information of previous studies and identify knowledge gaps, allowing, therefore, to understand the value of agroforestry systems for the conservation of native species, including amphibians and reptiles.

In our study, we performed a global meta-analysis to assess the ability of agroforestry systems to maintain amphibian and reptile diversity in human-modified landscapes. We predicted that agroforestry systems should have fewer abundance and species richness, and great dissimilarity in species composition than forests because the environmental complexity necessary for the maintenance and survival of herpetofauna species are changed in these systems (Macip-Ríos and Muñoz, 2008, Pineda and Halffter, 2004, Wanger et al., 2009). In fact, generalist species may thrive in agroforestry systems, whereas those sensitive to disturbances are less likely to utilize agroforests as supplementary habitat (Murrieta-Galindo et al., 2013, Vega-Agavo et al., 2021). This pattern, therefore, has the potential to create distinct communities of amphibians and reptiles when compared to agroforests with native forests. Nevertheless, due to the differences in life history between both taxa, we expected that the decline in amphibian diversity (i.e., richness and abundance) to be greater than in reptiles (Cordier et al., 2021, Palacios et al., 2013, Wanger et al., 2010). In fact, amphibian species present specific ecological traits, such as highly permeable skin, which make them more susceptible to desiccation, toxic chemicals, or bacterial and fungal infections, compared to reptiles, which have skin covered by protective scales (Catenazzi, 2015, Gibbons et al., 2000). We also assessed the impact of community parameter used by the studies (species richness or abundance) and the type of agroforestry system structure (simplified or complex) on the variation in effect size of amphibians and reptiles. In addition, we used meta-regression models to examine how the Hedges' g effect size is affected by the amount of forest cover around the agroforestry systems. Based on these additional analyzes we expected that:

i. Species richness of amphibians and reptiles in agroforests will decline more drastically than the abundance of individuals because some species do not possess the ability to inhabit agroforests, especially when this system is highly intensified (Palacios et al., 2013, Pineda and Halffter, 2004, Roach et al., 2021). In fact, common species, typically adapted to utilizing different environments and a wide variety of resources, may increase their relative abundance due to the ability to exploit human-modified habitats (Cervantes-López et al., 2022, Heinen, 1992, Whitfield et al., 2007). In addition, the disappearance of sensitive species may increase the availability of vacant niches that can be occupied by species adapted to disturbed habitats (Russildi et al., 2016).

ii. Agroforest presenting high complexity of local vegetation structure will show a higher species diversity (i.e., richness and abundance) than simplified systems due to a greater availability of the environmental conditions and resources necessary to support a wide variety of amphibians and reptiles (Gillespie et al., 2015, Macip-Ríos and Muñoz, 2008, Wanger et al., 2010).

iii. Agroforest inserted in more forested landscapes will show a greater species diversity of amphibians and reptiles given that the amount of forest cover can modulate agroforestry's ability to support more diverse herpetofauna assemblages (Faria et al., 2007, Vega-Agavo et al., 2021). Indeed, landscapes with high forest cover can provide habitats, breeding sites, resources and ideal environmental conditions which contribute to the survival of amphibians and reptiles.

Methods

Literature survey

Between April and May 2022, we carried out a bibliographic search in two online scientific databases - Scopus and Web of Science. The list of research studies, regardless the year of publication, was created using keyword combinations: (agroforest* OR agroecosystems* OR agroforestry*) AND (herpetofauna* OR herpetology* OR herptiles* OR "leaf-litter herpetofauna*" OR amphibian* OR Anura* OR Caudata* OR salamander* OR frog* OR toad* OR caecilian* OR reptiles* OR snakes* OR lizards*) AND (abundance* OR "species richness*" OR richness* OR diversity*). Subsequently, we used 'bibliometrix' package (Aria and Cuccurullo, 2017) in R software (version 4.1.2, R Core Team, 2021) for importing bibliographic data and eliminating duplicated studies. We also use Google Scholar (searches conducted until April 2023) to search for more recent articles, as well as gray literature, such as theses and dissertations.

Data inclusion criteria

In our study, we used data only of articles performed in agroforests defined as land-use systems in which perennial tree crops (e.g., coconut, rubber, coffee, vanilla, cocoa and others) are grown under a canopy of native and non-native trees (Nair et al., 2021). Therefore, we excluded studies that only included monocultures, rice paddy fields and/or plantations under the sun. In addition, we considered for the meta-analysis only studies that presented the following information: (i) comparison between native forest (primary and/or secondary forest) as control and agroforestry system as treatments; (ii) reporting separately the richness and/or abundance of amphibian and/or reptile species; and (iii) indicating a brief description of the vegetation structure and the composition of native trees of agroforest sampled. We also included a personal study about amphibian and reptile assemblages in cocoa agroforestry systems and native forest.

All studies that did not provide information necessary to calculate the average values and their standard deviations between treatment and control sites were excluded. As a result of this screening process (Fig. 1), we not included 57 studies from the 83 articles initially selected (39 from Scopus and Web of Science and 44 from Google Scholar). Finally, in our meta-analysis, we obtained 26 studies (24 studies on amphibians and 17 studies on reptiles) and 107 pairwise comparisons between controls and treatments (62 pairwise comparisons for amphibians and 45 on reptiles) (Fig. 1; Table A1). In particular, 3 studies were performed only with reptiles and 9 with amphibians, while 14 studies evaluated both groups (Table A1).

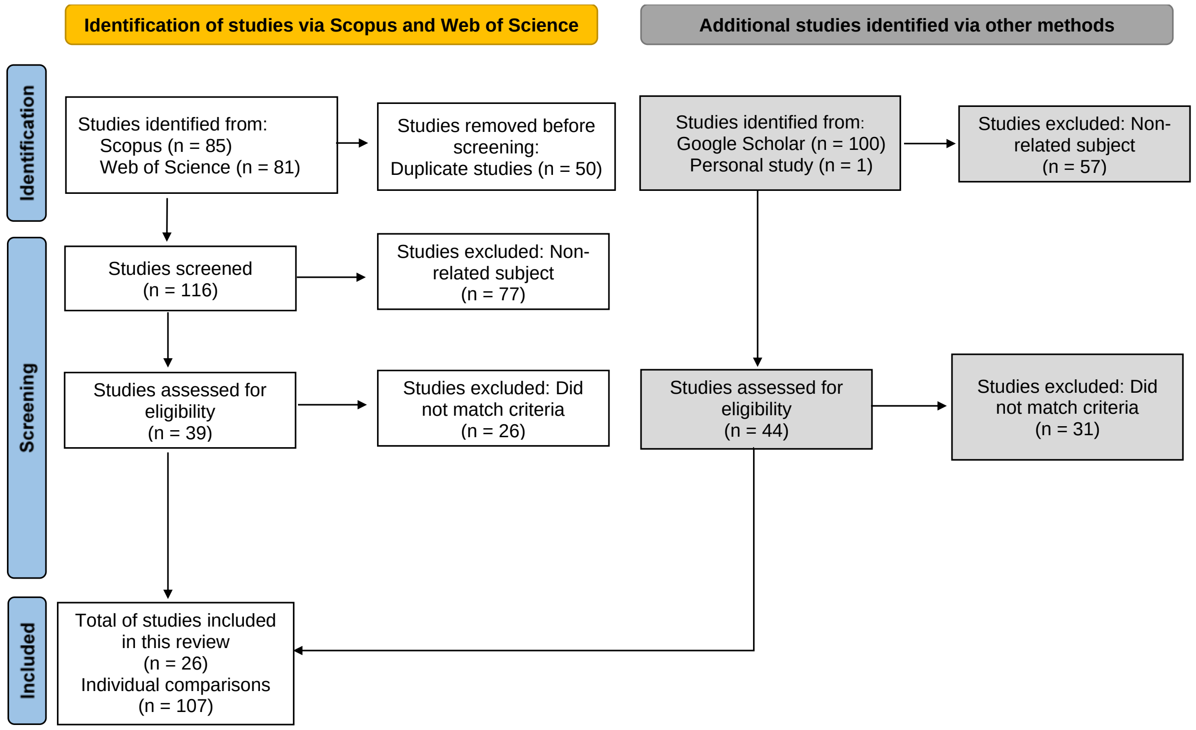

Figure 1. Flow diagram of studies obtained from online scientific databases (Scopus, Web of Science and Google Scholar). The layout of this diagram is suggested by the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 (Page et al., 2021).

Data extraction and analysis

For each study included in our meta-analysis, we extracted the sample size, which was estimated from the number of the sample units (e.g., number of transects or plots) in the control (forests) and treatment (agroforestry systems) sites, the mean value of the abundance and/or species richness, and the standard deviation. When the mean and standard deviation values were not reported directly in the articles, we extracted all information from figures using the GetData Graph Digitizer version 2.24 (http://getda ta-graph-digit izer.com/).

To calculate the effect size and confidence interval, we use Hedge's g-statistic (Borenstein et al., 2009, Gurevitch and Hedges, 1999) for each of the comparisons of amphibian and reptile diversity between the control and treatment sites. In our study, we used term “species diversity” to refer to the overall effect size (see Fig. 3) that was calculated considering all studies included in our meta-analysis, regardless of whether they were conducted with richness, abundance, or both parameters. In addition, comparisons were based on the information provided by each individual study. For instance, studies that assessed differences in the amphibian and reptile communities between agroforests and native forests provided at least 2 comparisons for each taxonomic group. Additionally, some studies made distinct comparisons between simplified agroforests and native forests, as well as between complex agroforests and natives forests. In summary, each comparison used in the meta-analysis is presented Table A1. In particular, Hedge's g-statistic estimates the standardized mean difference and variance between a control and treatment site and can be used in studies with a small sample size (Gurevitch and Hedges, 1999). Therefore, negative values of Hedge’s indicate a decrease richness/abundance in agroforests compared to forests and positive values indicate an opposite pattern. Effect sizes are considered significant if the confidence intervals do not overlap zero. In addition, we used a random-effects meta-analysis to calculated the mean effect size and 95% confidence intervals for all comparisons. We chose this method because the studies presented heterogeneity responses (amphibians: Q-test = 133.6, d.f. = 23, $p < 0.0001$; reptiles: Q-test = 91.1, d.f. = 16, $p < 0.0001$). Furthermore, since most of the studies included in our meta-analysis presented more than one comparison, we used a bootstrap method to avoid pseudo-replication bias and, consequently, enhance the robustness of our results. This procedure was performed by calculating the mean effect size per 10,000 replicates (with replacement), to generate a median effect size with 95% confidence intervals (Almeida-Rocha et al., 2017, Matuoka et al., 2020). All analyses were performed separately for amphibians and reptiles.

To assess the heterogeneity of effect sizes across studies, we used the bootstrap method with 10,000 replicates, as mentioned above. Based on the information provided by the studies, we obtained (Table 1): (i) the evaluated parameter of the community (abundance and species richness) of amphibians and/or reptiles; (ii) the type of agroforest; where simplified agroforests are dominated by exotic, shade-tree species, whereas complex agroforests are mainly composed of a wide variety of native tree species that retain part of the local structure of a forest, such as big trees that increase the shading of the understory layer. Therefore, complex agroforests presenting greater vertical stratification of vegetation that create a more favorable microclimate, as well as produce a greater amount of resources for the fauna (Greenberg et al., 2008); and (iii) percentage of forest cover surrounding each agroforestry system, using only studies that reported the geographic coordinates of sampling sites. We consider the sampling location within each of the agroforestry systems as the central point to estimate forest cover.

Table 1. Variables used in our meta-analysis to investigate the heterogeneity of effect sizes across studies. Therefore, all analysis is limited to a specific subset of studies and comparisons within certain categories.

Variables	Categories (n. of studies/n. of comparisons)
1. Parameter of the community	1.1 Abundance of individuals (amphibians: 17/22; reptiles: 12/15)
	1.2 Species richness (amphibians: 23/39; reptiles: 17/29)
2. Structure type of agroforestry system	2.1 Simplified agroforestry systems (amphibians: 14/29; reptiles: 9/21)
	2.2 Complex agroforestry systems (amphibians: 17/33; reptiles: 11/24)
3. Percentage of landscape forest cover	Average of forest cover around agroforestry systems measured in two different-sized landscapes (500 and 1000 m).

Given that the effect of landscape variables on biodiversity depends on the spatial scale at which predictors are measured (i.e. the so-called “scale of effect”; Fahrig, 2013, Jackson and Fahrig, 2015), we estimated forest cover in circular landscapes of 500 m and 1000 m radius around each sampling site within each agroforest. These spatial scales have been used in previous studies evaluating the impact of the forest cover on the species diversity of amphibians and reptiles (Ghosh and Basu, 2020, Russildi et al., 2016, Vega-Agavo et al., 2021). Then, to identify the landscape size in which forest cover presents a greater explanation on the effect size of amphibian and reptile assemblages (i.e. the scale of effect), we performed a multimodel inference using a ‘dmetar’ package in R software (Table A2).

To estimate the forest cover of each landscape size, we obtained the spatial information from the Global Forest Change (GFC) database (Hansen et al., 2013) using the packages ‘sp’ (Pebesma and Bivand, 2005), 'grid' (R Core Team, 2021) and 'rgdal' (Bivand et al., 2022) in R software. The GFC database provides Landsat images of approximately 30 m per pixel of forest cover values. To define the areas of forest surrounding each agroforest sites, we used a threshold of 60% canopy cover (Molinario et al., 2015, Potapov et al., 2012). This threshold value determines whether grid cells with a resolution of 30 m are classified as forest or non-forest (Hansen et al., 2013). Although the GFC database is an effective tool in distinguishing between native forests and plantations of exotic trees (such as eucalyptus plantations), especially when using thresholds > 30% (Altamirano et al., 2020, Burivalova et al., 2015 Potapov et al., 2017; Sannier et al., 2016), an overestimation of the amount of forest cover is likely to occur due to the difficulty of separating highly shaded agroforestry areas from native forests (Cunningham et al., 2019, Tropek et al., 2014). Therefore, we recognize that our estimate of forest cover may have considered both native forest and agroforestry systems.

In addition, as the studies used in our meta-analysis collected data in different years, we used the packages of ‘gfcanalysis’ (Zvoleff, 2020) to calculate the forest cover surrounding of agroforest for their respective survey year. Since all studies sampled multiple sites, we used the average amount of forest cover surrounding the sampled agroforests in each study. Finally, we used meta-regression models, with a permutation test in 10,000 permutations, to assess the influence of landscape forest cover on Hedges' g effect size using the ‘metafor’ package (Viechtbauer, 2010).

Finally, we used Sorensen's similarity index, which is based on species occurrence data, to assess the similarity of species composition of amphibian and reptile assemblages between agroforests and forests. The Sorensen values vary between zero (when agroforests and forests present completely different species assemblage) and 1 (when the environments are identical in species composition). Additionally, we used generalized linear models (GLM) with a Gaussian family and identity link function to assess the effect of agroforestry system type and landscape forest cover on Sorensen values for amphibian and reptile assemblages.

Publication bias

To evaluate the potential publication bias in our general meta-analyzes, we used the Rosenthal safety number (FSN) and the Trim-and-Fill approaches, using the ‘Metafor’ package (Viechtbauer, 2010). The first determines the quantity of studies that would be needed to the effect size to be non-significant ($p \geq 0.05$). If the fail-safe number is equal to or greater than 5*N + 10, where N represents the number of studies included in the review (Rosenthal, 1991), it indicates that a result should be considered robust to publication bias.

Otherwise, the Trim-and-Fill method estimates the number of missing studies needed to complete a symmetric funnel plot and then recalculates the mean effect size including these studies (Duval and Tweedie, 2000). For both approaches, we employed a bootstrap procedure considering a possible pseudo-replication bias. In addition, we used FSN analysis only for the overall meta-analyses that presented significant effects.

Results

Our meta-analysis of amphibians and reptiles in agroforestry systems were distributed in 12 countries (Fig. 2), whose Mexico (six studies) Madagascar (five studies), and Colombia (three studies) encompassed most of the investigations. Additionally, the majority of studies were conducted in the tropical region (amphibians, N = 23; reptiles, N = 14), with very few studies developed in the temperate region (amphibians, N = 1; reptiles, N = 3).

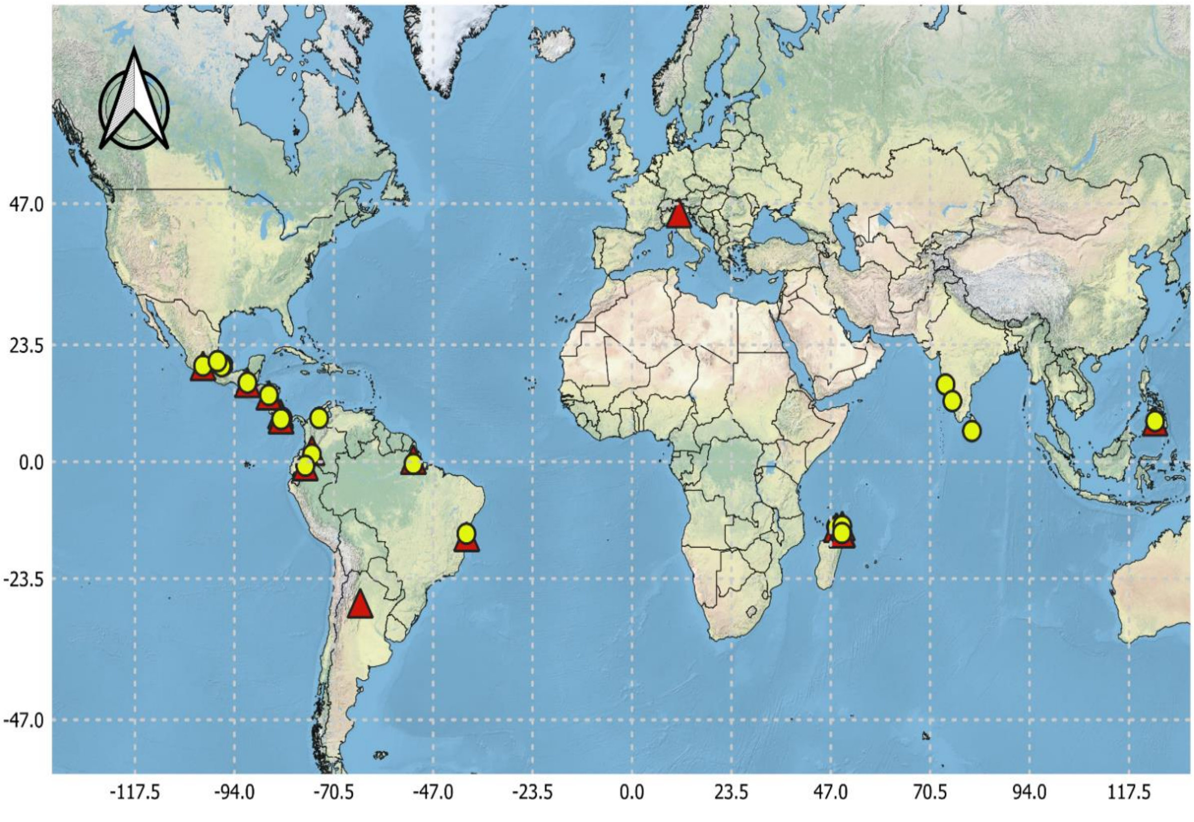

Figure 2. The geographic distribution of the 24 studies for amphibians (yellow circles) and 17 studies for reptiles (red triangles) included in the meta-analysis.

In amphibians, the overall mean effect size for the 24 studies and 62 comparisons was −0.62 [95% CI: −0.90; −0.35], indicating that agroforestry systems exhibit a lower amphibian diversity (i.e. including studies on richness and abundance) compared to natural forests. For reptiles, the overall mean effect size for the 17 studies and 45 comparisons was 0.03 [95% CI: −0.25; 0.31], evidencing that agroforests and forests show similar species diversity. According to Rosenthal's safety analysis, the number of studies required to obtained non-significant results in amphibians was 182 studies (FSN ≥ 130), evidencing that our results are robust and unaffected by publication bias. Nevertheless, Trim-and-Fill analyzes showed that there were no missing studies for both taxa, supporting the idea that our meta-analysis was unbiased (Fig. A1).

Our findings also highlighted that agroforestry systems were detrimental to the abundance and richness of amphibians when compared to forests (Fig. 3A). In contrast, agroforests present higher reptile abundance, but similar species richness, when compared to forests (Fig. 3A). We also observed that the structure type of the agroforestry systems did not change the general pattern of amphibian diversity (Fig. 3B). However, we detected that simplified agroforestry systems have a lower reptile diversity than forests (Fig. 3B).

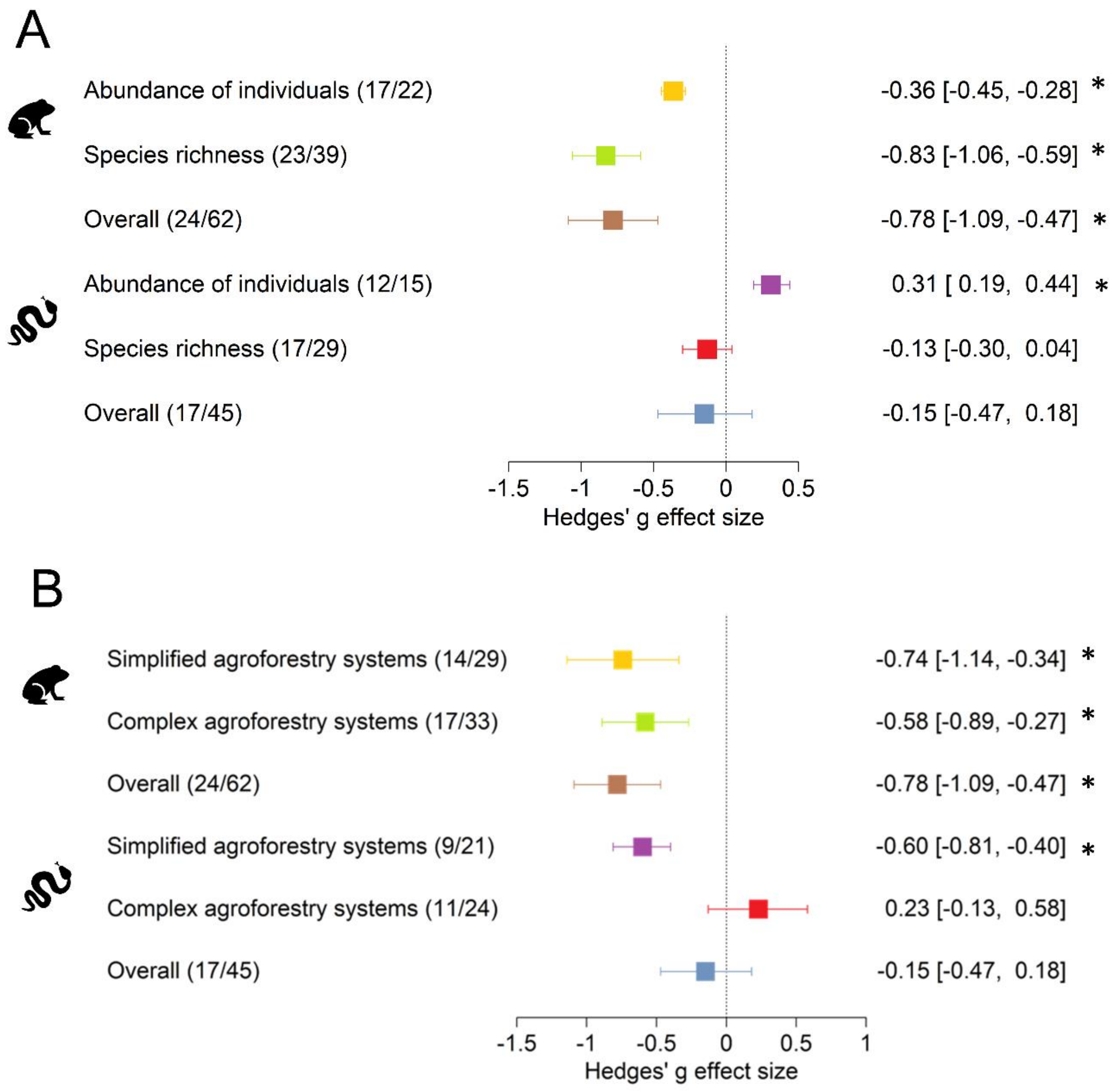

Figure 3. Bootstrapped effect sizes for amphibian and reptile assemblages analyzed by community parameters (A), and structure type of agroforestry system (B). In the forest plots, overall indicates the effect size estimated for all studies and comparisons for each taxonomic group. The vertical line evidences no difference between agroforest systems and native forests. Mean Hedges' g (squares) and the 95% CIs (lines) values are displayed on the right side (asterisks indicate statistical significance). On the left, categories of each group are presented with number of studies and individual comparisons in parentheses.

Our meta-regression models showed that the percentage of landscape forest cover (scale of 1000 m) exerts positive influence on the effect size of richness of reptile species (QM = 11.4, df = 1, p = 0.006; Table A2), evidencing that agroforestry systems when inserted in highly forested landscapes can harbor high species richness (Fig. 4). Similar result was observed when we considered the overall effect size of reptiles (Fig. A3).

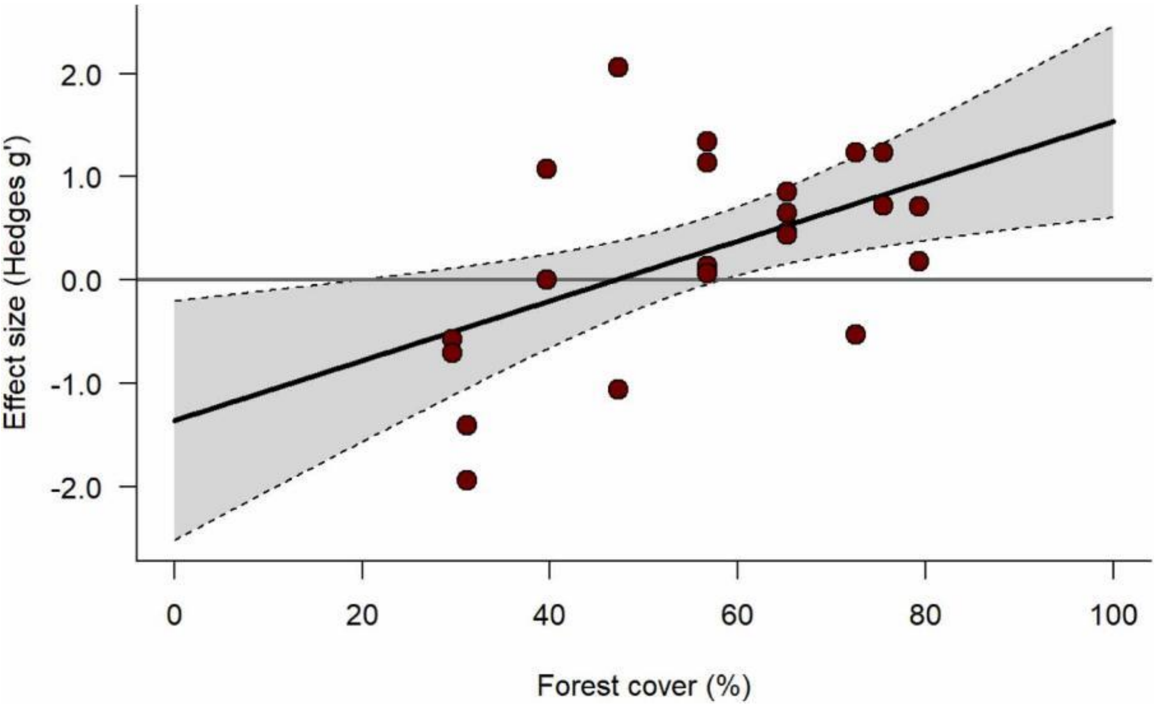

Figure 4. Meta-regression model used to explain the influence of the amount of landscape forest cover (scale of 1000 m) on effect sizes (Hedges' g) of richness of reptile species in agroforestry systems. The horizontal black line shows the value of Hedges' g = 0, where positive values indicate significant increases in species richness in agroforestry systems than compared to forests, while negative indicate the opposite. The thicker black line represents the slope of the meta-regression and the estimated confidence intervals are shown in gray.

We also observed that agroforests and native forests exhibit dissimilarity in the species composition of amphibians and reptiles. In particular, our results showed that the mean of similarity in species composition between agroforests and forests was 0.51 (± 0.21; standard deviation) for amphibians and 0.55 (± 0.17) for reptile assemblages. This result indicates that approximately half of the recorded species from both taxa differs between native forests and agroforestry systems. Also, GLM models evidenced that the type of agroforestry system and landscape forest cover did not affect the similarity of the species composition of amphibians and reptiles (Table A4).

Discussion

Our study provided evidence on the impact of agroforestry systems on herpetofauna in human-modified landscapes. In accordance with our predictions, we observed that amphibian assemblages in agroforestry systems presented a reduction in the abundance and species richness compared than forests. In contrast, agroforestry systems can support similar species richness and higher abundance of reptiles to native forests. These marked variations in the responses of amphibians and reptiles in agroforestry systems can be explained by the differences in their life histories and habitat requirements (Mendenhall et al., 2014, Palacios et al., 2013, Wanger et al., 2010). For instance, many amphibian species are more vulnerable to disturbances given that their permeable skin and strong dependence of humid environments (Catenazzi, 2015, Stuart et al., 2004), especially at the start of the breeding season (Becker et al., 2010). Conversely, reptile species are more adapted to living in disturbed environments due to their ecophysiological tolerance that increases their ability to resist higher temperatures (Palacios et al., 2013, Wanger et al., 2010). Based on Sorensen index, our findings also highlighted that half of the amphibian and reptile species observed in agroforests are different from those observed in native forests.

We showed that agroforestry systems exhibited a significant decrease in amphibian abundance and richness compared to native forests. Regarding amphibian richness, our results coincide with those documented by Palacios et al. (2013). However, their study indicates that the transformation of forests into agroforestry systems not exert effect in the abundance of species. In particular, the loss of species and individuals may be associated with the change in microclimatic conditions, decrease in the resources availability and the pollution caused by the use of agrochemicals in agroforestry systems (Ghosh and Basu, 2020, López-Bedoya et al., 2022, Pineda and Halffter, 2004, Wanger et al., 2023, Wanger et al., 2010, Wanger et al., 2009). Also, amphibians in agroforests can be infected by chytrid fungus (Murrieta-Galindo et al., 2014), which may lead to reduction in the abundance and richness in these systems. Conversely, tropical amphibians have been observed to be more susceptible to infection by the chytrid fungus in pristine environments than in disturbed habitats (Becker et al., 2017, Becker and Zamudio, 2011). This is mainly due to two factors: the higher richness of amphibians as potential hosts of the chytrid fungus and the favorable microenvironmental conditions in native habitat that facilitate the development of the fungus (Becker et al., 2017). These contradictions underscore the need for further research to understand the impact that infectious diseases can have on amphibian communities in agroforestry systems and natural forests. In addition, the application of agricultural chemicals can have harmful and even fatal consequences for amphibians living in agricultural areas (Ghosh and Basu, 2020, Krishna et al., 2005, Mendenhall et al., 2014, Rathod and Rathod, 2013, Wanger et al., 2023), also limiting the species occurrence and persistence of this group in human-modified environments.

The increase in the abundance of reptile in agroforestry systems may be associated to their greater detectability in less complex systems, since the simplicity of these environments could facilitate the observation of reptiles (Elbahi et al., 2023). In addition, the conservation of native elements in agricultural areas can increase the number of microhabitats and available resources for many reptile species (Biaggini and Corti, 2015, Cervantes-López et al., 2022, Macip-Ríos and Muñoz, 2008). For instance, several studies have indicated that a greater diversity of shade trees and a higher proportion of litter in cocoa agroforestry systems can be decisive environmental factors for a greater number of reptiles (Heinen, 1992, Lieberman, 1986, Orozco et al., 2016). Conversely, human-made structures, such as stone walls, artificial ponds, and old buildings can help certain common reptile species providing a microhabitat and favoring the increase of its population density in these agricultural systems (Henderson and Powell, 2001). Likewise, other possible explanations for the higher abundance of reptiles in agroforestry systems could be linked to the high ecophysiological tolerance of this group, which enables species to explore ecological niches within agricultural areas (Evans, 2019, Gardner et al., 2007, Macip-Ríos and Muñoz, 2008). Therefore, reptile species with greater tolerance to more disturbed habitat environments could be responsible for increasing abundance within agroforestry systems. Our findings align with those of Palacios et al. (2013), who also reported higher abundance and similar richness of reptiles in agroforestry systems compared to native forests.

We observed that the type of agroforestry systems (complex or simplified) does not change the overall effect size of the amphibian assemblage. Regardless of the agroforestry type, the richness and abundance of amphibians in these agricultural systems was significantly lower than in forests. Indeed, the decrease in native trees, mainly big trees, and hence the reduction in shading, in simplified agroforestry systems leads to decrease in favorable microhabitats, such as leaf litter and water bodies, necessary for the reproduction of amphibian species and their eventual increase in the number of individuals (Deheuvels et al., 2014, Wanger et al., 2010). However, the observed reduction in the amphibian diversity in complex agroforests was unexpected because several studies have documented that these systems can host large portion of amphibian species, including forest-dweller species (Cervantes-López et al., 2022, Evans, 2019, Heinen, 1992, Lieberman, 1986). This result can be associated the use of management practices, such as the removal of shrubs, herbs or lianas, in the lower stratum, that change environmental conditions and microhabitats (Rice and Greenberg, 2000). Therefore, while a complex agroforestry system may provide improved environmental conditions and resources for amphibian assemblages compared to simplified agroforests, the removal or alteration of understory vegetation can disrupt the availability of suitable breeding sites and food sources and, as a consequence, cause a decrease in the number of individuals and species. This disruption is particularly detrimental to the survival of numerous amphibian species, especially those that have a specialization for forest habitats (Bos and Sporn, 2012, Wanger et al., 2009). Also, the presence of exotic trees, especially in simplified agroforestry systems, could generate potential negative impacts on the abundance and richness of amphibian species (López-Bedoya et al., 2022). In particular, exotic trees could contribute to the reduction in resource availability by simplifying tree diversity (Martin and Murray, 2011). In addition, a review study found that the presence of non-native plants can impact the reproductive process of amphibians (Bucciarelli et al., 2014, Martin and Murray, 2011).

For reptiles, simplified agroforestry systems exhibit reduced structural complexity of vegetation due to the reduction of native trees, which affects the conditions and resources that many species need to survive and persist in agricultural areas (Wanger et al., 2010). Also, simplified agroforestry systems frequently use intensive management techniques including the use agrochemicals, such as pesticides (Moguel and Toledo, 1999), which may harm reptiles directly (Marco et al., 2004, Monagan et al., 2017, Simbula et al., 2021, Wanger et al., 2023) or indirectly by affecting the availability of invertebrates that reptiles depend on for diet (Monagan et al., 2017). Moreover, previous studies have also found that agroforestry systems with higher presence of native vegetation and more structurally complex systems can result in greater number of ecological niches and microhabitats, which are indispensable for the persistence of a high diversity of reptile species (Cervantes-López et al., 2022, Macip-Ríos and Muñoz, 2008, Wanger et al., 2010). Other studies have shown that the presence of exotic plants, commonly recorded in simplified agroforest, can present negative effect on reptile assemblages (López-Bedoya et al., 2022). In particular, changes in habitat structure resulting from the presence of exotic plants can affect thermal conditions and the availability of shelter and food resources, posing challenges for reptile species to survive in severely disturbed environments (Martin and Murray, 2011).

According to our meta-regression models, we observed that landscape forest cover had only a positive influence on effect size of reptile richness, indicating that agroforestry systems inserted in more forested landscapes harbor a high reptiles richness. Our findings can be attributed to three probable explanations. First, landscapes with high forest cover increase the amount of habitat available for a broad diversity of species, including those species dependent on specific resources (Cabral et al., 2021, Calamari et al., 2018, Faria et al., 2007, Morante-Filho et al., 2015, Vega-Agavo et al., 2021). Regarding the habitat amount hypothesis (see Fahrig, 2013), there is a positive correlation between the quantity of habitat in a landscape and the species richness within a local patch. Therefore, the presence of forested habitats surrounding agroforests allows this agricultural system to harbor reptile species with diverse ecological needs, resulting in an increase in species richness in highly forested landscapes. Second, a high proportion of forest cover also increases landscape connectivity (Tscharntke et al., 2008), enabling species to utilize various environments (e.g., habitat spillover hypothesis, see Dunning et al., 1992) within of the landscape, and consequently exploit a wide range of niches and ecological resources available (Faria et al., 2007, Rice and Greenberg, 2000). Finally, agroforests surrounded by large forest fragments, may present an increase in the availability of prey, such as rats and other small rodents (Caudill et al., 2014, Chaiyarat et al., 2020, Weist et al., 2010), and therefore favor several species of reptiles, such as snakes. Our results are in agreement with those reported by Faria et al. (2007) who observed that cocoa agroforestry inserted in more forested landscapes may harbor high species diversity, including reptile species. Also, our result highlighted that agroforest can harbor a rich reptile assemblage only when inserted in landscapes with more than 50% forest cover (Fig. 4). Therefore, the ability of agroforestry systems to maintain reptile diversity is modulated by the landscape forest amount, indicating that preserving forest remnants is essential for the conservation of native species in human-modified landscapes (Arroyo-Rodríguez et al., 2020, Faria et al., 2007)

It is noteworthy that the presence of forest cover did not yield a positive impact on the effect size of amphibian assemblages, despite previous studies suggesting that high values of forest cover surrounding agroforestry systems can promote an increase in species richness and abundance (Faria et al., 2007, Vega-Agavo et al., 2021). This our results could be attributed to the fact that the amphibian assemblages in agroforestry systems consist of species that exhibit varying responses to environmental disturbances and tend to present a smaller number of individuals than species inhabiting native forests (Evans, 2019, Vega-Agavo et al., 2021). For instance, structurally simplified agroforests are likely to be inhabited by species that are more resilient to habitat disturbances, including those capable of thriving in agroforests located in severely deforested landscapes (Fulgence et al., 2021, Sankararaman et al., 2021). Given that amphibians exhibit a high dependency on specific habitat characteristics, such as the presence of water bodies, and have low dispersal capacity (Gibbons et al., 2000), it is likely that local factors are more important in determining species diversity than the amount of landscape forest cover.

Our study also has revealed distinct amphibian and reptile species compositions in agroforestry systems compared to native forests. These differences in species composition can be attributed to structural changes within agroforestry systems and species' preferences for specific habitats (Evans, 2019, Gardner et al., 2007). Indeed, changes in understory vegetation caused by agroforestry practices can alter the microenvironmental conditions and create barriers that impact the distribution and persistence of these species (Fulgence et al., 2021, Macip-Ríos and Muñoz, 2008, Pineda et al., 2005). In this context, numerous studies have indicated that agroforestry systems are more likely to host species of amphibians and reptiles of generalist habits (Beirne et al., 2013, Pineda et al., 2005, Pineda and Halffter, 2004, Vega-Agavo et al., 2021, Wurz et al., 2022). For instance, in coffee agroforestry systems in Mexico (Lara-Tufiño et al., 2019, Murrieta-Galindo et al., 2013, Pineda and Halffter, 2004), it was observed that the reduction of canopy cover has a direct impact on the presence of forest specialist frogs, such as *Incilius macrocristatus*, *Charadrahyla taeniopus*, *Megastomatohyla mixomaculata*, *Craugastor alfredi*, and *Craugastor decorates*, which are adapted to more closed canopy conditions. Conversely, generalist anurans, such as Incilius valliceps and *Eleutherodactylus cystignathoides*, are commonly recorded in agroforestry systems (Cervantes-López et al., 2022, Murrieta-Galindo et al., 2013). Therefore, changes in local features, such as canopy cover, can impact the species richness, as well as the species composition of the amphibian assemblages in agricultural systems. Also, in study conducted in Madagascar (Blumgart et al., 2017), forest specialist reptiles, such as Brookesia minima, B. ebenaui, *Lygodactylus madagascariensis* and *Thamnosophis stumpffi*, were found exclusively in forested areas, while generalist species, such as *Boophis tephraeomystax*, *Gephyromantis granulatus*, *Calumma nasutum*, and *Phelsuma laticauda*, were recorded particularly in coffee agroforests. It is also important to emphasize that several studies have documented the presence of forest specialist reptiles and amphibians in agroforestry systems. (Blumgart et al., 2017, Kudavidanage et al., 2012). For instance, several species of forest specialist amphibians (*Craugastor palenque*, *C. laticeps,* and *Incilius campbelli*) and reptiles (*Anolis capit*o, *A. uniformis*, *Lepidophyma flavimaculatum*) have been commonly observed in cocoa agroforests in Mexico (Cervantes-Lopez et al., 2022; Heinen, 1992; Wanger et al., 2010).

Conclusions

Our study provides compelling evidence of the impact of agroforestry systems on amphibian and reptile assemblages in human-modified landscapes. In particular, agroforestry systems can negatively impact amphibian assemblages, but maintain a similar richness of reptiles, and a greater abundance, than native forests. However, simplified agroforests show a decrease in the richness of reptiles, indicating that increasing the complexity of the vegetation structure in these systems, via enhance of the diversity of native trees and consequent greater vertical stratification and shading, can assist to maintain of species diversity (i.e. values of abundance and species richness similar to those observed in native forests) (Macip-Ríos and Muñoz, 2008, Wanger et al., 2010). However, in the face of increasing agricultural expansion in natural landscapes it is crucial to identify all those features that can enhance the conservation quality of ecologically friendly matrices for species diversity (Arroyo-Rodríguez et al., 2020, Perfecto and Vandermeer, 2008). Therefore, management practices that contribute to diversifying agroforestry systems, and consequently increasing their structural complexity, can support species diversity, especially reptiles. Additionally, ceasing forest loss is urgently necessary for the conservation of herpetofauna. In fact, in more forested landscapes (> 50%), agroforests can even assist in increasing reptile richness. Also, our study has revealed notable variations in amphibian and reptile species composition between agroforestry systems and native forests. This result may be associated with changes in the vegetation structure of agroforestry systems and the dependency on certain habitat characteristics by amphibian and reptile species. However, we emphasized that about half of the amphibian and reptile assemblage is shared between native forests and agroforests, highlighting that this agricultural system can act as supplementary habitat for a significant portion of species from both groups. Finally, it is important to note that the vast majority of studies included in this meta-analysis were conducted in tropical regions. For this reason, we emphasize the need for more studies in temperate region, covering both taxa, to accurately assess whether the response of species in agroforestry systems varies between biogeographic regions.

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CRediT authorship contribution statement

José Morante-Filho: Writing – review & editing, Validation, Supervision, Conceptualization. Martín de Jesús Cervantes-López: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

No potential conflict of interest was reported by the authors.

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Supporting information

Table A1. Final dataset 26 studies and 107 pairwise comparisons of amphibian and reptile diversity between agroforestry systems and native forests. Each individual comparison is characterized by the study reference, the taxonomic group and the moderator variables (parameter of the community, structure type of agroforestry systems, geographic location and forest cover measured in spatial scales of 500 and 1000 m) used to verify the heterogeneity of the overall effect sizes. We indicated the number of samples per control (N_{cont}) and treatment (N_{treat}), their mean values (M_{cont} and M_{treat}) and their respective standard deviations (SD_{con} and SD_{treat}).

Study (year)	**N_{treat}**	**M_{trear}**	**SD_{treat}**	**N_{con}**	**M_{con}**	**Sd_{con}**	**Taxonomic group**	**Community parameters**	**Type of structure of agroforestry systems**	**Forest cover 500m**	**Forest cover 1000m**	**Sorensen index**
Beirnei et al. (2013)	8	13.33	5.7	15	11.4	5.02	Amphibians	Abundance	Complex	NA	NA	NA
Beirnei et al. (2013)	8	2.6	0.63	15	4.63	1.46	Amphibians	Richness	Complex	NA	NA	0.56
Beirnei et al. (2013)	8	1.26	0.96	15	1.14	1.17	Reptiles	Abundance	Complex	NA	NA	NA
Beirnei et al. (2013)	8	1	0.65	15	1	1.02	Reptiles	Richness	Complex	NA	NA	0.61
Biaggini et al. (2015)	27	0.56	0.667	18	0.6	0.68	Reptiles	Richness	Simplified	NA	NA	0.5
Biaggini et al. (2015)	27	0.805	1.03	18	0.977	1.286	Reptiles	Abundance	Simplified	NA	NA	NA
Blumgart et al (2017)	10	18.3	33.8	11	20.4	29.4	Amphibians	Abundance	Simplified	74.32	62.10	NA
Blumgart et al (2017)	10	6.9	9.3	11	6.4	6.8	Amphibians	Richness	Simplified	74.32	62.10	0.75
Blumgart et al (2017)	11	4.8	9.4	11	20.4	29.4	Amphibians	Abundance	Simplified	79.82	70.64	NA
Blumgart et al (2017)	11	2.7	4.9	11	6.4	6.8	Amphibians	Richness	Simplified	79.82	70.64	0.94
Blumgart et al. (2017)	10	48.6	58.5	11	20.4	14.6	Reptiles	Abundance	Simplified	74.32	62.10	NA
Blumgart et al. (2017)	10	21.2	23.8	11	12.5	10.7	Reptiles	Richness	Simplified	74.32	62.10	0.77
Blumgart et al. (2017)	11	71.2	79.4	11	20.4	14.6	Reptiles	Abundance	Simplified	79.82	70.64	NA
Blumgart et al. (2017)	11	20.6	22.8	11	12.5	10.7	Reptiles	Richness	Simplified	79.82	70.64	0.66
Brüning et al. (2018)	2	2.9	0.2	2	1.9	0.4	Amphibians	Richness	Complex	60.60	66.16	NA
Brüning et al. (2018)	3	3.007	0.7	2	1.9	0.4	Amphibians	Richness	Simplified	60.60	66.16	NA
Study (year)	**N_{treat}**	**M_{trear}**	**SD_{treat}**	**N_{con}**	**M_{con}**	**Sd_{con}**	**Taxonomic**	**Community**	**Type of**	**Forest**	**Forest**	**Sorensen**

Study (year)	N_{treat}	M_{trear}	SD_{treat}	N_{con}	M_{con}	Sd_{con}	Taxonomic group	Community parameters	Type of structure of agroforestry systems	Forest cover 500m	Forest cover 1000m	Sorensen index
Cervantes-López et al. (2022)	12	24.6	15.3	12	11.9	6.2	Amphibians	Abundance	Complex	86.70	79.45	NA
Cervantes-López et al. (2022)	12	6.4	1.6	12	5.2	2.3	Amphibians	Richness	Complex	86.70	79.45	0.8
Cervantes-López et al. (2022)	12	54.3	11.6	12	47.1	7.5	Reptiles	Abundance	Complex	86.70	79.45	NA
Cervantes-López et al. (2022)	12	6	1.8	12	5.7	1.4	Reptiles	Richness	Complex	86.70	79.45	0.57
Coria et al. (2016)	7	22	7	7	15	5	Reptiles	Abundance	Complex	13.47	28.97	NA
Coria et al. (2016)	7	4	1	7	4	1	Reptiles	Richness	Complex	13.47	28.97	0.66
Cruz-Elizaldi et al. (2016)	12	14.6	7.4	12	16	12.7	Amphibians	Abundance	Complex	NA	NA	NA
Cruz-Elizaldi et al. (2016)	12	3	1.7	12	2.5	1.2	Amphibians	Richness	Complex	NA	NA	0.52
Deheuvels et al. (2014)	36	2.3	0.3	8	3.6	0.7	Amphibians	Richness	Complex	NA	NA	NA
Deheuvels et al. (2014)	36	3.9	0.3	8	2.9	0.7	Reptiles	Richness	Complex	NA	NA	NA
Díaz-Ricaurte et al. (2020)	3	197	48.6	3	94	8.1	Amphibians	Abundance	Simplified	52.13	40.88	NA
Díaz-Ricaurte et al. (2020)	3	11	1	3	13	1	Amphibians	Richness	Simplified	52.13	40.88	0.75
Díaz-Ricaurte et al. (2020)	3	73.7	10.4	3	94	8.1	Amphibians	Abundance	Simplified	48.61	56.92	NA
Díaz-Ricaurte et al. (2020)	3	7.3	2.3	3	13	1	Amphibians	Richness	Simplified	48.61	56.92	0.71
Evans (2019)	2	6	0	3	9	1	Amphibians	Richness	Simplified	76.13	75.59	NA
Evans (2019)	2	6.8	2.8	3	1.1	0.9	Amphibians	Abundance	Simplified	76.13	75.59	NA
Evans (2019)	2	23.5	3.5	3	18.6	2.5	Reptiles	Richness	Simplified	76.13	75.59	NA
Evans (2019)	2	12.9	1.7	3	9.5	4.01	Reptiles	Abundance	Simplified	76.13	75.59	NA

Study (year)	N_{treat}	M_{trear}	SD_{treat}	N_{con}	M_{con}	Sd_{con}	Taxonomic group	Community parameters	Type of structure of agroforestry systems	Forest cover 500m	Forest cover 1000m	Sorensen index
Faria et al. (2007)	6	36.03	14.8	6	49.7	30	Amphibians	Abundance	Complex	NA	NA	NA
Faria et al. (2007)	6	6.7	1.5	6	7.2	2.2	Amphibians	Richness	Complex	NA	NA	0.92
Faria et al. (2007)	4	41.5	22.4	4	36.4	38.3	Amphibians	Abundance	Complex	NA	NA	NA
Faria et al. (2007)	4	4.8	0.5	4	5.9	1.02	Amphibians	Richness	Complex	NA	NA	0.67
Faria et al. (2007)	6	24.7	4.9	6	14.4	4.8	Reptiles	Abundance	Complex	NA	NA	NA
Faria et al. (2007)	6	4.5	1.4	6	5.2	0.6	Reptiles	Richness	Complex	NA	NA	0.9
Faria et al. (2007)	4	31.01	7.5	4	22.1	4.9	Reptiles	Abundance	Complex	NA	NA	NA
Faria et al. (2007)	4	4.5	1.2	4	5.25	1.2	Reptiles	Richness	Complex	NA	NA	0.53
Fulgence et al. (2021)	10	5.1	0.5	10	9.3	1.2	Amphibians	Richness	Complex	NA	NA	0.17
Fulgence et al. (2021)	20	5.4	0.7	10	9.3	1.2	Amphibians	Richness	Simplified	NA	NA	0.16
Fulgence et al. (2021)	10	5.1	1.1	10	9.3	1.2	Amphibians	Richness	Simplified	NA	NA	0.15
Fulgence et al. (2021)	10	5.1	0.5	10	6.03	1.4	Amphibians	Richness	Complex	NA	NA	0.4
Fulgence et al. (2021)	20	5.4	0.7	10	6.03	1.4	Amphibians	Richness	Simplified	NA	NA	0.44
Fulgence et al. (2021)	10	5.1	1.1	10	6.03	1.4	Amphibians	Richness	Simplified	NA	NA	0.29
Fulgence et al. (2021)	10	8.9	2.5	10	9.9	1.4	Reptiles	Richness	Complex	NA	NA	0.41
Fulgence et al. (2021)	20	6.9	1.5	10	9.9	1.4	Reptiles	Richness	Simplified	NA	NA	0.31
Fulgence et al. (2021)	10	6	1.2	10	9.9	1.4	Reptiles	Richness	Simplified	NA	NA	0.3
Fulgence et al. (2021)	10	8.9	2.5	10	9.9	1.7	Reptiles	Richness	Complex	NA	NA	0.63
Fulgence et al. (2021)	20	6.9	1.5	10	9.9	1.7	Reptiles	Richness	Simplified	NA	NA	0.66
Fulgence et al. (2021)	10	6	1.2	10	9.9	1.7	Reptiles	Richness	Simplified	NA	NA	0.61
Gardner et al. (2007)	5	142.8	85.1	5	103	20.1	Amphibians	Abundance	Complex	NA	NA	NA
Gardner et al. (2007)	5	2.6	0.5	5	9.2	13.7	Amphibians	Richness	Complex	NA	NA	0.37
Gardner et al. (2007)	5	142.8	85.1	5	102	58.81	Amphibians	Abundance	Complex	NA	NA	NA
Gardner et al. (2007)	5	2.6	0.5	5	8.2	1.48	Amphibians	Richness	Complex	NA	NA	0.28
Gardner et al. (2007)	5	151.4	16.1	5	136.2	48.01	Reptiles	Abundance	Complex	NA	NA	NA
Gardner et al. (2007)	5	6.6	1.5	5	3.4	2.1	Reptiles	Richness	Complex	NA	NA	0.49
Gardner et al. (2007)	5	151.4	16.1	5	99.8	30.35	Reptiles	Abundance	Complex	NA	NA	NA
Gardner et al. (2007)	5	6.6	1.5	5	8	1.73	Reptiles	Richness	Complex	NA	NA	0.57

							group	**parameters**	**structure of agroforestry systems**	**cover 500m**	**cover 1000m**	**index**
Hending et al. (2022)	6	2.67	1.66	9	5.33	4.02	Amphibians	Richness	Complex	45.83	44.44	0.47
Hending et al. (2022)	6	3	1.102	9	5.33	4.02	Amphibians	Richness	Simplified	28.65	24.57	0.36
Hending et al. (2022)	6	9.5	2.93	9	15.11	4.17	Reptiles	Richness	Complex	45.83	44.44	0.57
Hending et al. (2022)	6	7.67	2.49	9	15.11	4.17	Reptiles	Richness	Simplified	28.65	24.57	0.46
King et al. (2007)	7	0.8	1.4	5	1.6	1.5	Amphibians	Abundance	Simplified	76.82	70.67	NA
King et al. (2007)	7	0.8	1.4	5	1.4	1.5	Amphibians	Richness	Simplified	76.82	70.67	0.5
King et al. (2007)	7	4.1	1.7	5	6.2	5.4	Reptiles	Abundance	Simplified	76.82	70.67	NA
King et al. (2007)	7	5.2	1.8	5	2.8	1.8	Reptiles	Richness	Simplified	76.82	70.67	0.59
Komanduri et al. (2023)	10	4.1	1.66	10	4.1	2.38	Amphibians	Richness	Complex	20.46	22.01	0.62
Kudavidanage et al. (2012)	25	51.04	27.2	25	52.7	17	Amphibians	Abundance	Complex	NA	NA	NA
Kudavidanage et al. (2012)	25	8.2	2.4	25	6.6	2.75	Amphibians	Richness	Simplified	NA	NA	0.34
Mendenhall et al. (2014)	24	10.9	10	6	76.7	46.7	Amphibians	Abundance	Simplified	NA	NA	NA
Mendenhall et al. (2014)	24	3.2	2.2	6	8.3	3.1	Amphibians	Richness	Simplified	NA	NA	0.55
Mendenhall et al. (2014)	24	15.8	15.4	6	48.9	45.1	Reptiles	Abundance	Simplified	NA	NA	NA
Mendenhall et al. (2014)	24	5.6	5.3	6	10.8	1.3	Reptiles	Richness	Simplified	NA	NA	0.19
Moreno-Arias and Quintero-Corzo (2015)	8	21.9	9.2	16	30.9	17.2	Reptiles	Abundance	Complex	38.35	30.93	NA
Moreno-Arias and Quintero-Corzo (2015)	8	6.1	1.2	16	7.3	1.8	Reptiles	Richness	Complex	38.35	30.93	0.58
Murrieta-Galindo et al. (2013)	2	221	28.1	2	206	130.1	Amphibians	Abundance	Complex	84.85	75.03	NA
Murrieta-Galindo et al. (2013)	2	12.5	0.7	2	12	7.1	Amphibians	Richness	Complex	84.85	75.03	0.5
Study (year)	**N_{treat}**	**M_{trear}**	**SD_{treat}**	**N_{con}**	**M_{con}**	**Sd_{con}**	**Taxonomic group**	**Community parameters**	**Type of structure of**	**Forest cover**	**Forest cover**	**Sorensen index**

									agroforestry systems	500m	1000m	
Murrieta-Galindo et al. (2013)	2	112	25.4	2	206	130.1	Amphibians	Abundance	Simplified	77.81	73.84	NA
Murrieta-Galindo et al. (2013)	2	8	1.4	2	12	7.1	Amphibians	Richness	Simplified	77.81	73.84	0.62
Nuñeza et al. (2010)	5	18.8	14.2	6	52	36.13	Amphibians	Abundance	Simplified	NA	NA	NA
Nuñeza et al. (2010)	5	7.2	2.77	6	10.67	4.03	Amphibians	Richness	Simplified	NA	NA	0.66
Nuñeza et al. (2010)	5	11.66	10.17	6	13	14.61	Amphibians	Abundance	Simplified	NA	NA	NA
Nuñeza et al. (2010)	5	6.83	5.23	6	5.4	4.4	Amphibians	Richness	Simplified	NA	NA	0.54
Pineda and Halffter (2004)	3	31.6	3.8	5	40.2	9.7	Amphibians	Abundance	Complex	77.86	72.19	NA
Pineda and Halffter (2004)	3	8.3	1.5	5	10.4	1.8	Amphibians	Richness	Complex	77.86	72.19	0.66
Pineda et al. (2005)	3	34.7	7.2	3	46.7	10.7	Amphibians	Abundance	Complex	76.73	70.76	NA
Pineda et al. (2005)	3	9	1.7	3	10.7	2.5	Amphibians	Richness	Complex	76.73	70.76	0.38
Rathod and Rathod (2013)	5	35.13	4.38	5	43.13	4.02	Amphibians	Abundance	Complex	48	50	NA
Rathod and Rathod (2013)	5	9.33	2.35	5	10.81	1.25	Amphibians	Richness	Complex	48	50	0.7
Rathod and Rathod (2013)	5	25.81	5.11	5	43.13	4.02	Amphibians	Abundance	Simple	48.00	50.00	NA
Rathod and Rathod (2013)	5	8.14	1.5	5	10.81	1.25	Amphibians	Richness	Simplified	48	50	0.73
Vega-Agavo et al. (2021)	8	11.75	14.5	4	6.2	2.9	Amphibians	Abundance	Complex	50.88	47.51	NA
Vega-Agavo et al. (2021)	8	2.1	0.6	4	1.7	1.7	Amphibians	Richness	Complex	50.88	47.51	0.38
Vega-Agavo et al. (2021)	8	46.5	21.3	4	6.5	3.7	Reptiles	Abundance	Complex	50.88	47.51	NA
Vega-Agavo et al. (2021)	8	1.7	1.4	4	3.5	1.9	Reptiles	Richness	Complex	50.88	47.51	0.75
Wurz et al. (2022)	10	4.6	1.8	10	9.3	2.31	Amphibians	Richness	Complex	66.18	63.35	0.17
Wurz et al. (2022)	10	4.6	1.8	10	5.1	2.07	Amphibians	Richness	Complex	66.18	63.35	0.4
Wurz et al. (2022)	20	4.55	1.19	10	9.3	2.31	Amphibians	Richness	Simplified	56.93	55.54	0.2
Wurz et al. (2022)	20	4.55	1.19	10	5.1	2.07	Amphibians	Richness	Simplified	56.93	55.54	0.52

Wurz et al. (2022)	10	9.4	3.43	10	9.8	2.15	Reptiles	Richness	Complex	66.18	63.35	0.31
Wurz et al. (2022)	10	9.4	3.43	10	9.6	2.75	Reptiles	Richness	Complex	66.18	63.35	0.29
Wurz et al. (2022)	20	6.85	2.13	10	9.8	2.15	Reptiles	Richness	Simplified	56.93	55.54	0.63
Wurz et al. (2022)	20	6.85	2.13	10	9.6	2.75	Reptiles	Richness	Simplified	56.93	55.54	0.64

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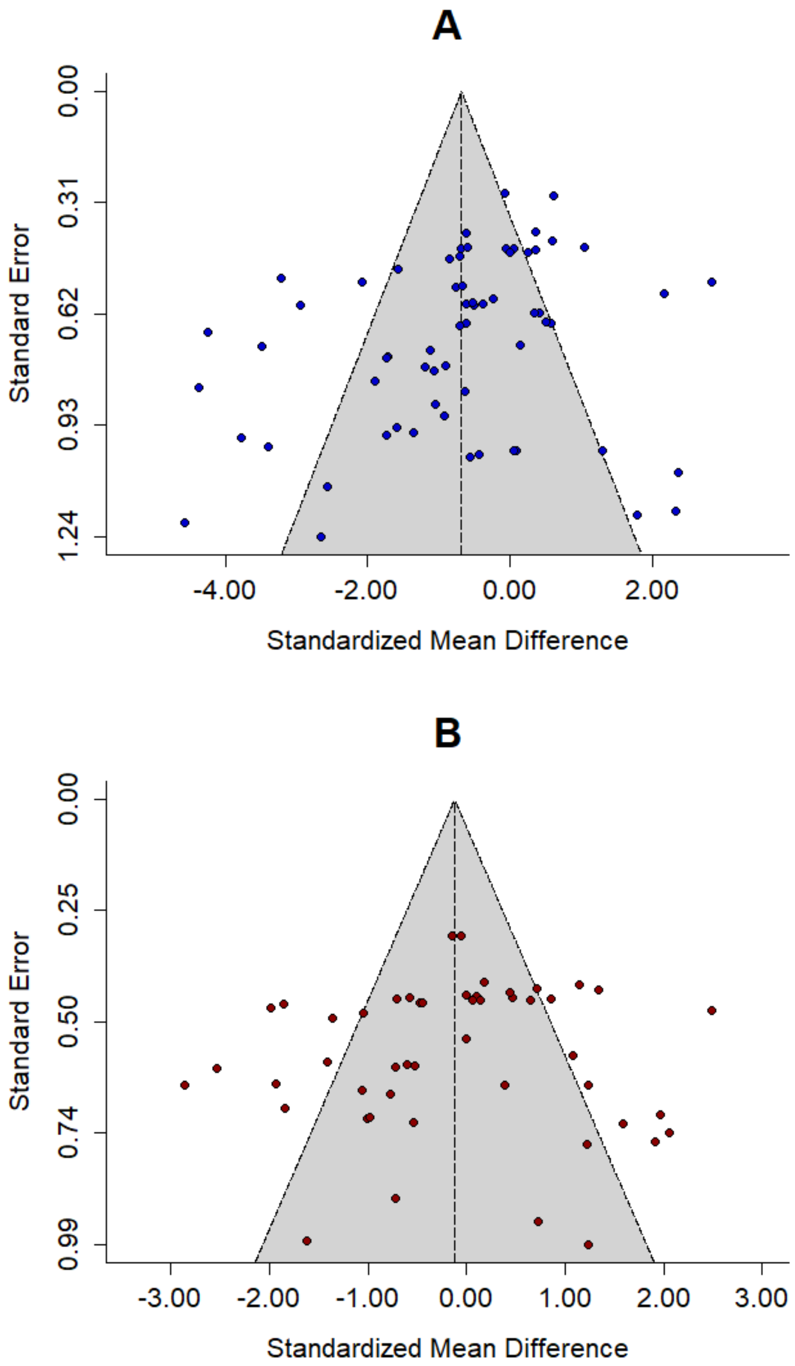

Figure A1. Funnel plot of the observed effect sizes (Hedges' g) or outcomes (x-axis) of the amphibians (A) and reptiles (B) plotted against the corresponding standard errors. The gray area bordered by dashed lines represents 95% confidence interval. The funnel plot indicates the absence of bias and heterogeneity for both groups.

Table A2. Results of meta-regression models evaluating the relationship between the landscape forest cover (scale of 500 and 1000 m radius) and the effect size (Hedge's g) for the abundance, richness and diversity (considering the abundance and richness together) of amphibian and reptile communities. The table shows the omnibus test number (QM) with its degrees of freedom (df), the *p*-values with permutations (at 10,000 replications) for each model and the predictor importance (i.e. landscape size at 500 and 1000 m) for each of the meta-regression model. In addition, to define the best spatial scale (i.e., 500 or 1000m), we used the average importance of the predictor in all models. This analysis indicated that the landscape size with the highest importance for almost all meta-regression models was 1000 m.

Taxonomic group/variables	**Landscape size (m)**	**QM (df = 1)**	***p*-values**	**Predictor importance**
Amphibian diversity	500	0.58	0.45	0.53
Amphibian diversity	1000	0.82	0.37	**0.56**
Amphibian abundance	500	0.004	0.94	0.36
Amphibian abundance	1000	0.006	0.93	**0.37**
Amphibian richness	500	0.67	0.42	0.4
Amphibian richness	1000	0.98	0.32	**0.53**
Reptile diversity	500	6.97	0.01	0.52
Reptile diversity	1000	8.2	0.009	**0.67**
Reptile abundance	500	0.007	0.9	0.59
Reptile abundance	1000	0.02	0.887	**0**.59
Reptile richness	500	9.06	0.01	0.45
Reptile richness	1000	11.4	0.006	**0.73**

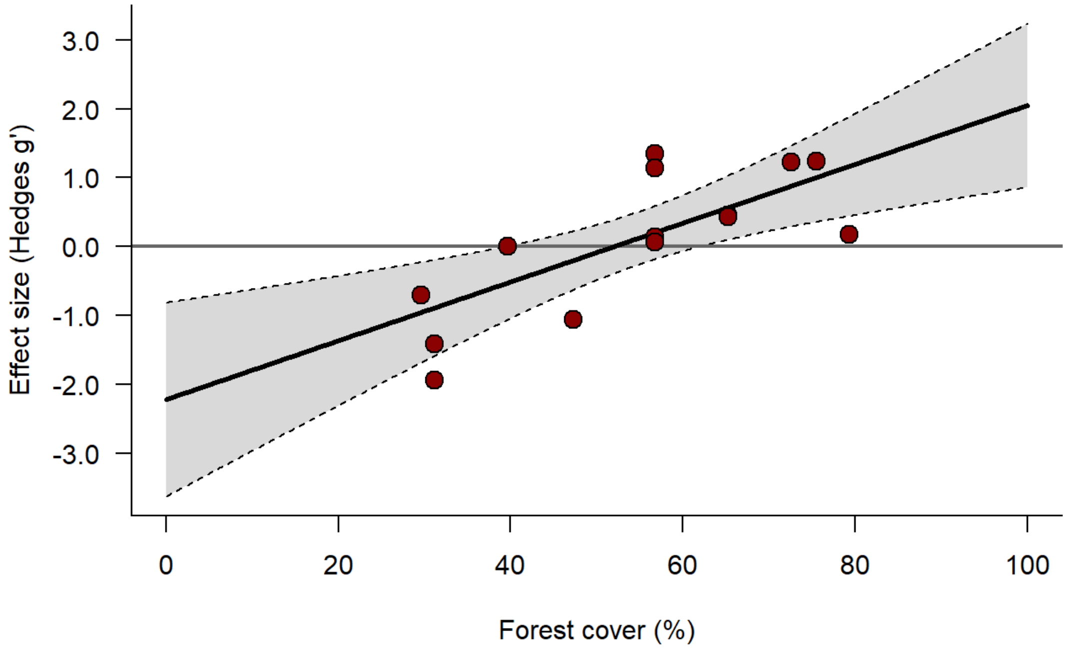

Figure A3. Meta-regression model used to explain the influence of the amount of landscape forest cover (scale of 1000 m) on effect sizes (Hedges' g) of the diversity of reptile assemblages in agroforestry systems. The horizontal black line shows the value of Hedges' g = 0, where positive values indicate significant increases in species richness in agroforestry systems than compared to forests, while negative indicate the opposite. The thicker black line represents the slope of the meta-regression and the estimated confidence intervals are shown in gray.

Table A4. Generalized Linear Models evaluating the effect of differences in amphibian and reptile community composition on agroforestry system types and forest cover.

Amphibians	**Model fit**
Sorensen index ~ Type of agroforestry systems	$\chi^2(1) = 0.01$, p = 0.85
Sorensen index ~ Forest cover (1000 m radio)	$\chi^2(1) = 0.0002$, p = 0.55
Reptiles	**Model fit**
Sorensen index ~ Type of agroforestry systems	$\chi^2(1) = 0.04$, p = 0.6
Sorensen index ~ Forest cover (1000 m radio)	$\chi^2(1) = 0.0004$, p = 0.85

Capítulo 2. Landscape predictors are more important than local factors in determining multiple dimensions of amphibian and reptile diversity in shaded cocoa agroforests

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Landscape predictors are more important than local factors in determining multiple dimensions of amphibian and reptile diversity in shaded cocoa agroforests

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Abstract

Context High rates of deforestation have prompted discussions on the use of agricultural systems for biodiversity conservation. Although agroforests are recognized as supplementary habitats for many species, it is still unclear whether this agricultural system can maintain multiple dimensions of species diversity.

Objectives We investigated the impact of landscape and local factors on the taxonomic, functional and phylogenetic richness and diversity of the herpetofauna in 30 cocoa agroforests located in three different regions of the Atlantic Forest.

Methods We used Hill's numbers in orders 0 and 1 to estimate the richness and diversity of each dimension of amphibian and reptile communities. Using model selection approach, we evaluate the influence of landscape and local factors on the different dimensions of diversity of both groups.

Results For amphibians, we observed that pasture cover positively affects taxonomic richness and diversity, as well as phylogenetic richness. In contrast, forest edge density and number of forest fragments negatively affect richness and functional diversity, respectively. We also observed that the region with high forest cover exhibited lower amphibian functional richness. For reptiles, we found that forest cover and edge density positively affect species richness. We also noted that forest cover and edge density positively affect phylogenetic richness and diversity, respectively. Regarding local factors, only humidity positively affected functional richness and diversity, while temperature had a negative effect on reptile functional richness.

Conclusions Our study showed that the landscape context in which cocoa agroforests are located modulates the ability of this agricultural system to harbor multiple dimensions of amphibian and reptile diversity in human-modified landscapes.

Keywords: Agroforest systems, Anthropogenic landscapes, Fragmentation, Habitat loss, Herpetofauna, Land-sharing, Tropical Forest.

Introduction

The increasing loss and degradation of natural habitats, primarily driven by human activities, have led to the decline of global biodiversity (Young et al. 2016). In response to the biodiversity crisis, some strategies have been proposed to ensure both long-term species diversity conservation and agricultural demands. For example, conservationists argue that productive lands and areas designated for conservation should be spatially separated within landscapes (Green et al. 2005). This strategy, known as land sparing, assumes that by intensifying agricultural practices, higher productivity can be achieved in smaller areas, thereby facilitating the conservation of large native remnants (Green et al. 2005). In contrast, another strategy, known as land-sharing, proposes that human-modified landscapes be composed of mosaics of different intermixed environments, including biodiversity-friendly agricultural areas and native habitats (Green et al. 2005; Phalan et al. 2011). In this strategy, less intensified agricultural systems such as agroforests could be used as supplementary habitat for native species, in addition to facilitating organism movement between native habitat fragments (Perfecto and Vandermeer 2010). Based on this, biodiversity-friendly agricultural matrices can assist in the species conservation and therefore should be considered in management measures in such landscapes (Arroyo-Rodríguez et al. 2020).

Among the agricultural systems, shaded agroforests—such as those used for vanilla, cocoa, and coffee—hold the highest ecological value due to their complex vegetation structure (Altieri 1999; Rice and Greenberg 2000; Hending et al. 2023). In such agroforests, agricultural crops are planted under the canopy of native trees that can serve as resources for species (Nair et al. 2021). Therefore, these systems can mitigate the negative effects of habitat loss and degradation by providing supplementary habitats for many species, such as arthropods (Manson et al. 2024), mammals (Ferreira et al.

2020), birds (Cabral et al. 2021), amphibians and reptiles (Cervantes-López et al. 2022). However, local and landscape characteristics can influence the capacity of the agroforest systems to maintain species diversity. For example, shaded cocoa agroforests located in highly deforested regions show a distinct composition of anuran and lizard species compared to those located in more forested regions, as evidenced by a study conducted in northeastern Brazil (Faria et al. 2007). In addition, in a global meta-analysis was evidenced that landscape forest cover can increase the ability of agroforests to support a high diversity of reptile species (Cervantes-López and Morante-Filho 2024). Conversely, when inserted into highly degraded landscapes, i.e., composed of inhospitable matrices, such as pasture, and with a reduced and fragmented amount of native forests, agroforests may harbor a simplified community of native species (Faria et al. 2007; Vega-Agavo et al. 2021). Therefore, the landscape context in which agroforests are located can play a crucial role in the conservation value of these agricultural systems.

The local characteristics of agroforests can also affect their ability to harbor native species. Along a management gradient, agroforests may differ in microclimatic conditions due to variations in local vegetation characteristics, leading to changes in abundance, diversity, and species composition (Altieri 1999; Rice and Greenberg 2000). Indeed, several studies have observed that in shaded agroforests, such as cocoa (Faria et al. 2007; Wanger et al. 2010; Cervantes-López et al. 2022), coffee (Macip-Ríos and Muñoz-Alonso 2008; Lara-Tufiño et al. 2019), and vanilla (Fulgence et al. 2022; Hending et al. 2023), maintaining local environmental characteristics similar to native forests can stabilize abiotic conditions and thus provide a wide variety of microhabitats and resources necessary for native species survival. For example, the presence of dense leaf litter, along with branches and trunks on the ground, and a more closed canopy due to large native trees, exerts a positive effect on the abundance and diversity of understory herpetofauna in cocoa agroforests (Heinen 1992; Pineda and Halffter 2004; Wanger et al. 2010). Therefore, management intensity can directly impact local vegetation characteristics, and hence the ability of agroforests to harbor native species (Macip-Ríos and Muñoz-Alonso 2008; Fulgence et al. 2022).

Overall, most studies examining the impact of agroforests on conservation use metrics related only to taxonomic diversity, particularly species richness and abundance (Pineda and Halffter 2004; Macip-Ríos and Muñoz-Alonso 2008; Wanger et al. 2010; Cervantes-López et al. 2022; Fulgence et al. 2022). However, taxonomic diversity assumes that all species are equally important for community structure, underestimating the role of functional traits and evolutionary history of species in community resilience to environmental disturbances (Cardoso et al. 2014). Moreover, functional effect traits are closely linked to the ecological roles performed by species and, therefore, can determine the influence of species on ecosystem functioning (Hernández-Ordóñez et al. 2019; Álvarez-Grzybowska et al. 2020). Therefore, to provide a deeper understanding of the ecological value of the agroforest systems for conservation, it is essential to incorporate multiple dimensions of the diversity, including the evaluation of the species' functional traits (functional diversity) and their evolutionary relationships (phylogenetic diversity) (Álvarez-Grzybowska et al. 2020; Zabala-Forero and Urbina-Cardona 2021).

Here, we assessed the impact of both landscape (native forest cover, pasture cover, forest edge density, and number of forest fragments) and local factors (number of shade trees, cocoa trees and understory plants, number of fallen trunks, canopy cover, air temperature, and relative humidity) on the taxonomic, functional, and phylogenetic richness and diversity of amphibian and reptile communities in cocoa agroforest systems. In particular, these agroforests are located in three regions in the Brazilian Atlantic Forest, characterized by distinct land use contexts. We predicted (i) a positive effect of the landscape forest amount and number of forest fragments on all dimensions of richness and diversity of amphibian and reptile species, especially in the more deforested region. Specifically, landscapes composed of the high forest amount and large number of forest fragments should provide a greater amount of available habitat (Fahrig 2013; Almeida-Gomes et al. 2019), thus enabling agroforests to harbor a rich community of amphibians and reptiles (Faria et al. 2007; Russildi et al. 2016; Vega-Agavo et al. 2021; Cervantes-López and Morante-Filho 2024), composed of functionally and phylogenetically distinct species (Almeida-Gomes et al. 2019; Rincón-Aranguri et al. 2023; Leal-Santos et al. 2024). Furthermore, the increase in the number of forest fragments can enhance landscape permeability and thus facilitate species dispersal (Santizo-Nanduca et al. 2023; Leal-Santos et al. 2024). We expected (ii) a negative effect of the landscape pasture amount on all dimensions of richness and diversity of both taxonomic groups, especially because pasture areas can limit species dispersal and exacerbate edge effects (Pineda and Halffter 2004; Isaacs and Urbina-Cardona 2011). We also predicted (iii) a positive effect of edge density on the taxonomic richness and diversity of both groups, but not on functional and phylogenetic metrics. In fact, this pattern is expected because species' responses to human disturbance are mediated by a strong phylogenetic signal (Frishkoff et al. 2014; Campos et al. 2019). Therefore, landscapes dominated by forest edges may exhibit a proliferation of generalist species, which are phylogenetically closely related and share many ecological traits (Carvajal-Cogollo and Urbina-Cardona 2015). Finally, we expected that (iv) the increase in complexity of the local vegetation structure in cocoa agroforests, characterized by a greater number of understory shrubs, deep layer of leaf litter and fallen trunks on the ground, as well as a high number of shade trees that will create a denser canopy, will positively affect multiple dimensions of richness and diversity amphibian and reptile species. In fact, complex agroforest systems can provide a greater variety of ecological niches, food resources, and suitable microclimates (e.g., presenting moderate air temperature and high relative humidity), which would contribute to the formation of highly diverse communities of both groups (Macip-Ríos and Muñoz-Alonso 2008; Wanger et al. 2010; Cervantes-López et al. 2022).

Methods

Study area

This study was conducted in the southeastern of the Bahia state, Brazil, an area dominated by remnants of Atlantic Forest. According to Köppen's classification, the predominant climate in the study area is hot and rainy for most of the year, without a defined dry season, although a relatively less rainy period occurs between December and March (Thomas et al. 1998). The average annual temperature is 24°C, and the average annual precipitation varies between 1,500 and 2,000 mm. The characteristic vegetation types of this portion of the Atlantic Forest are defined as Dense Ombrophilous Forest, marked by distinct vertical stratification and high diversity of many taxonomic groups, including plants (Thomas et al. 1998), mammals (Ferreira et al. 2020), birds (Morante-Filho et al. 2015), amphibians (Haddad et al. 2013; Dias et al. 2014), and reptiles (de Freitas 2014; Tozetti et al. 2017). Despite harboring a significant amount of native forests (about 40%), the study area has undergone profound land use changes, forming anthropic landscapes composed primarily of forest fragments, shaded cocoa (*Theobroma cacao*) agroforests, eucalyptus (*Eucalyptus sp.*) and rubber (*Hevea brasiliensis*) plantations, and pasture areas (Morante-Filho et al. 2016).

In the southern Bahia, shaded cocoa agroforests are traditionally known as cabruca, where cocoa is planted in the understory of Atlantic Forest remnants and shaded by native and exotic trees (Faria et al. 2007). We selected 30 shaded cocoa agroforests, each separated by a minimum distance of 2 km, with sizes ranging from 4 to over 100 hectares, and evenly distributed across three regions with different land uses (Fig. 1). The northernmost region, referred to as the High Agroforest Cover (HAC) region (Fig. 1b), exhibits 42% forest cover and has 39% of its area designated for cocoa agroforests. Open areas, primarily comprising cattle pastures, constitute only 8% of the matrix this region. In the central portion of the study area, designated as the High Forest Cover (HFC) region (Fig. 1c), is observed a significant extent of forest cover, totaling 53%, primarily concentrated within the Una Biological Reserve and the Una Wildlife Refuge. These protected areas composed an area of 34,804 hectares. The landscape matrix is dominated by cocoa agroforest systems (23%) and cattle pastures (12%). In contrast, the southernmost region, denoted as the Low Forest Cover (LFC) region (Fig. 1d), shows extensive deforestation, with only 32% forest cover. The landscape this region is notably more homogeneous, characterized by the prevalence of pastures (30%), eucalyptus plantations (6%), and a minimal presence of cocoa agroforest systems (17%).

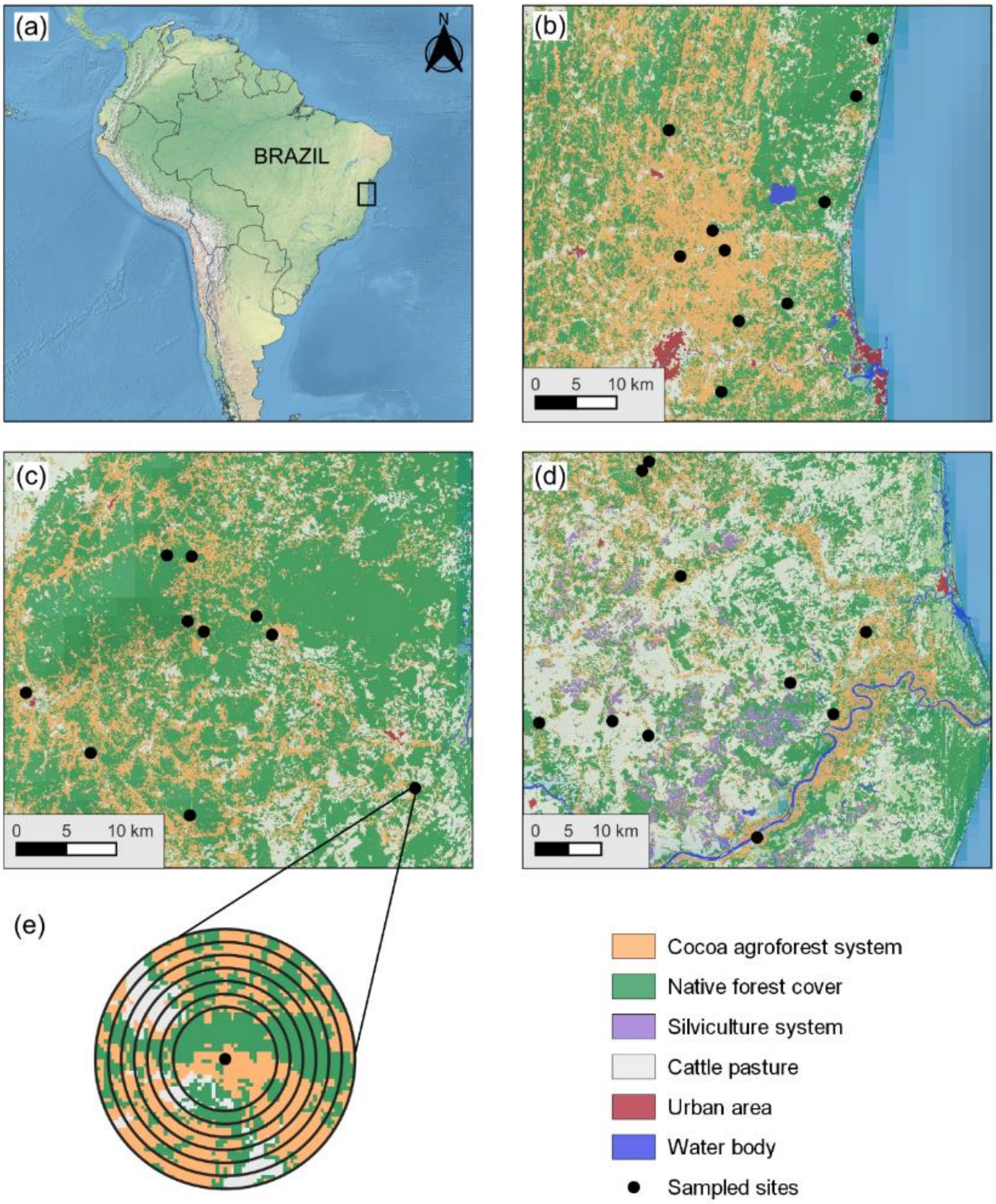

Figure 1. Location of the 30 shaded cocoa agroforest systems (black dots) sampled in southern Bahia state (a), Brazil, in three regions with different land use contexts. The northernmost region (b), called the High Agroforest Cover region, is composed of moderate forest cover and a high amount of cocoa agroforest systems. In the central portion of study are, referred as High Forest Cover region (c), present high forest cover and moderate amount of cocoa agroforest systems. The southernmost region, called as the Low Forest Cover region (d), is dominated by open areas destined for pasture, and a low amount of forest remnants and cocoa agroforest systems. We also present a diagram (e) illustrating the design of the seven landscapes (varying of 400 m to 1000 m radii),

which we used to determine the influence of landscapes predictors on amphibian and reptile metrics.

Landscape predictors

In our study, we used the patch-landscape approach (Fahrig 2013), in which response variables (diversity metrics) were sampled within cocoa agroforests, and landscape predictors were estimated around each agroforest. Using QGIS software (version 3.34.3, (QGIS Development Team 2024) and mapping recently developed by MapBiomas project that estimated the area designated to cocoa agroforests in 83 municipalities in the Bahia state (MapBiomas Cacau 2023), we estimated four landscape metrics: the amount of native forest (i.e., forest cover) and pasture, the number of forest fragments, and forest edge density (i.e., the forest edge length of the landscape divided by the total landscape area in hectares). In particular, we selected these predictors because several studies have demonstrated their effects on amphibian and reptile diversity (Russildi et al. 2016; Vega-Agavo et al. 2021; Rincón-Aranguri et al. 2023; Leal-Santos et al. 2024).

Since we don't know a priori which landscape size is most suitable for assessing the effects of predictors on the multiple dimensions of reptile and amphibian diversity, we used different landscape sizes (Jackson and Fahrig 2015). For this, we estimated each landscape metric in seven buffers around the center of the sampling point of each agroforest, ranging from 400 to 1000 m in radius, at intervals of 100 m (Fig. 1e). The smallest landscape had a radius of 400 m because it is the minimum size capture variation in the amount of native forest. We also avoided using landscapes larger than 1000 m due to overlap with other landscapes, which could create spatial dependency. Then, we employed the “multifit” function (Huais 2018) in R software (R Core Team 2023) to identify the best scale for assessing the effect of each landscape metric on our response variables (see results in Appendix 1 of the supplementary material).

Local factors

In each shaded cocoa agroforest system, we established three parallel plots measuring 50 m x 3 m, separated from each other by 20 m. Within these plots, environmental variables, such as number of shade trees and cocoa trees, number of fallen trunks, number of understory plants, leaf litter depth, canopy cover, air temperature, and relative humidity, were sampled to describe the local structure commonly associated with amphibian and reptile communities (Wanger et al. 2010; Cervantes-López et al. 2022). We counted the number of shade trees with a minimum diameter at breast height (DBH) of ≥ 10 cm, encompassing both native and exotic species, as well as number of cocoa trees. Additionally, we counted the number of fallen trunks with a diameter of ≥ 10 cm. We also assessed canopy cover using a Motorola E7 smartphone equipped with a hemispherical fisheye lens. Three photos per plot, spaced at least 25m apart, were taken at a height of 4m to exclusively capture canopy of shade trees, excluding cocoa trees. We used the Gap Light Analysis Mobile Application (Glama) to estimate the average Canopy Cover index of each agroforest (Tichý 2016). The count of understory plants (10–100 cm in height) was conducted in three subplots measuring 0.5 m x 0.5 m distributed at 0, 25, and 50 m within each plot, comprising seedlings, herbaceous plants, and small shrubs. However, creeping plants were excluded from our assessment. In each subplot, we estimated the litter depth at the beginning, middle, and end by using a ruler to measure the distance from the ground to the maximum height of the litter layer. Moreover, we installed a data logger at a height of 1.5 m in the center of a plot in each agroforest to record air temperature and relative humidity. These climatic variables were recorded for five consecutive days during two field seasons (see section below on herpetofauna sampling).

Herpetofauna surveys

The sampling of herpetofauna was performed by two researchers during two field seasons (from January to April and from September to December 2023). Using the method of Visual Encounters Surveys (Doan 2003), we searched for amphibian and reptile species in different microhabitats (e.g., under rocks, fallen logs, streams, and leaf litter) within the cocoa agroforests. At each field station, the herpetofauna of each agroforest was sampled for 2 days at two distinct periods for 6 h: diurnal (10:00–13:00) and nocturnal (18:00–21:00). Thus, the sampling effort per agroforest was 24 h (2 field seasons × 2 days × 6 h). All individuals of both taxa observed in the field were directly identified using field guides for amphibians and reptiles of the Atlantic Forest (Argôlo 2004; Haddad et al. 2013; de Freitas 2015). Species not identified during sampling were collected for later identification by specialists and subsequently deposited in the Zoology Museum of the Universidade Estadual de Santa Cruz—UESC. The scientific nomenclature follows Amphibian Species of the World (Frost 2024) and The Reptile Database (Uetz and Stylianou 2018). The abundance of amphibian and reptile species in each cocoa agroforest was estimated by the sum of individual records observed over the four sampling days. Although the sampling method adopted in our study is widely used in ecological studies of amphibians and reptiles (Cabrera-Guzmán and Reynoso 2012; de Cervantes-Lopez et al. 2022; Ríos-Orjuela et al. 2024), and the likelihood of recording the same individuals in tropical habitats is low (Urbina-Cardona et al. 2006; Cabrera-Guzmán and Reynoso 2012; Almeida-Gomes et al. 2022), we sought to minimize this probability by sampling in different locations within the agroforests on consecutive days during the same field season.

Species traits and phylogenetic tree

We used available literature to obtain ecological traits of amphibians (Oliveira et al. 2017; Liedtke et al. 2022; Moura et al. 2024) and reptiles (Moura et al. 2024), which were subsequently used to estimate functional diversity. The selected traits comprised numerical, such as body size and biomass, and categorical data, including activity time, microhabitat, and reproductive mode. However, because biomass was strongly correlated ($r = 0.8$) with body size in amphibians, we excluded biomass from the functional diversity calculations for this group. All traits were chosen based on their relevance in previous studies on amphibians (Almeida-Gomes et al. 2019; Álvarez-Grzybowska et al. 2020) and reptiles (Badillo Saldaña et al. 2024; Leal-Santos et al. 2024). In fact, such traits provided insight into the life history of the species, their interactions with the environment, and the potential functions and services performed by them (Cortés-Gomez et al. 2015; Almeida-Gomes et al. 2019). More details on the description of each ecological trait, including its functional importance, can be found in Appendix 2.

We also used available phylogenetic trees for amphibians (Jetz and Pyron 2018) and reptiles (Tonini et al. 2016) to estimate the phylogenetic relationship between species within each taxonomic group. Although it was possible to use the best available phylogenetic tree for amphibians (Jetz and Pyron 2018), for reptiles it was necessary to create a consensus tree. For this, we generated a Maximum Credibility Clade (MCC) consensus tree from 10,000 sampled phylogenies using the “mcc” function in the “phangorn” package (Schliep et al. 2017). Furthermore, for recently described species that have not yet been included in available trees, such as the anurans *Bahius bilineatus*, *Phyllodytes magnus*, *Pristimantis* sp., and *Vitreorana baliomma*, we used the evolutionary age of the congeners (Ouchi-Melo et al. 2018). To assess the presence of phylogenetic signal among our ecological traits, we used the D value (Fritz & Purvis 2010) for categorical traits (e.g., activity time, microhabitat, and reproductive mode) and Blomberg's K (Blomberg et al. 2003) for continuous traits (e.g., body length and body mass). In particular, $D = 1$ suggests that a trait is randomly distributed across the phylogenetic tree, $D = 0$ indicates a clustered distribution consistent with a Brownian motion model, and D values below 0 reflect even stronger clustering. For Blomberg's K, values $= 0$ indicates no phylogenetic signal, and $K = 1$ suggests a neutral structure (Brownian motion). Significant values of $K < 1$ and $K > 1$ indicate a weaker or stronger signal, respectively, than would be expected by chance under Brownian motion model. These analyses were carried out using the "caper" (Orme et al. 2023) and "phytools" (Revell 2024) package of the R software (R Core Team 2023).

Taxonomic, functional, and phylogenetic metrics

We used the true diversity index or Hill numbers (Jost 2006) to estimate the multiple dimensions of diversity for amphibians and reptiles. In particular, Hill numbers is an approach commonly used in ecological studies (Russildi et al. 2016; Cervantes-López et al. 2022; Cardoso et al. 2023) to estimate species diversity, in which the index value depends on the parameter "q" that is sensitive to species abundance. In our study, we employed Hill numbers with parameters (q) 0 and 1 to assess multiple dimensions of amphibian and reptile communities. Specifically, q=0, which this not account to species abundance, assigns disproportionate weight to rare species, thus capturing taxonomic richness. Conversely, q=1 weights each species based on its abundance within the community, favoring more abundant species by assigning them higher weights than rare species (Chao and Jost 2012). Therefore, q=1 represents taxonomic diversity.

For functional metrics, while q=0 assigns equal weight to all species, reflecting functional richness based on the number of ecological traits in the community, q=1 represents the effective number of equally abundant species, which gives more weight to the ecological traits of common species (i.e., functional diversity, Chao et al. 2014). In addition, for phylogenetic metrics, q=0 represents phylogenetic richness, indicating the number of lineages within a community, while q=1 expresses the effective number of phylogenetic branches weighted by species abundance (i.e., phylogenetic diversity, Chao et al., 2014).

In our study, we used the package “Inext3d” (Chao et al. 2021) of the R software (R Core Team 2023) to estimate taxonomic, functional, and phylogenetic richness and diversity of both groups.

Data analyses

We first assessed the accuracy of our inventory of amphibian and reptile species using the coverage estimator recommended by Chao and Jost (2012), which estimates the proportion of the total number of individuals in a community that belong to the species represented in the sample. In particular, assessing sample completeness is crucial for minimizing potential biases, thereby enabling more accurate inferences about the true diversity estimates of a given community (Chao et al. 2021). Our amphibian inventories were highly accurate with our sampling coverage, averaging (± standard deviation) 0.97 ± 0.015 per cocoa agroforest (Appendix 3). However, sampling coverage values for reptile species showed high variation among agroforests (minimum = 0.61; maximum = 0.98; Appendix 3). Based on these results, we used the observed data to calculate the taxonomic, functional, and phylogenetic richness and diversity of amphibian communities, and estimated values using a sample coverage of 0.83 for all sampled agroforests to calculate the multiple dimensions of reptile diversity. We adopted this value (0.83) because it represents the average sample completeness for reptile inventories across all cocoa agroforests.

We used generalized linear models, and Poisson (only in taxonomic richness of amphibians) or Gamma error distribution with a log-link function, to assess the effect of landscape (i.e., amount of native forest and pasture, forest edge density and number of forest fragments) and local predictors (i.e., number of cocoa trees, shaded trees and understory plants, number of fallen trunks, leaf litter depth, canopy cover, air temperature, and relative humidity) on the taxonomic, functional, and phylogenetic richness and diversity of amphibians and reptiles. For this, we first evaluated the correlation between pairs of predictors using the Pearson correlation coefficient and removed variables, such as leaf litter depth, with coefficients ≥ 0.70 (Appendix 4). Additionally, because some variables present a non-normal distribution, we applied logarithmic to local variables, such as number of cocoa trees, shade trees and understory plants, and number of fallen trunks. Then, we used a multi-model approach (Grueber et al. 2011), with function dredge of the package “MuMIn” (Bartoń 2023), to construct all possible combinations of models containing from one to four predictor variables.

Specifically, our complete models were composed of four predictor variables, which included two landscape predictors (i.e. one variable of landscape composition [native forest cover or pasture cover] and one of configuration landscape [forest edge density or number of forest fragments]), one local predictor and the study region (HAC, HFC and LFC) as categorical variable. Furthermore, we developed a null model to assess whether the models were better than expected at random. In our models, we did not test the interaction between environmental predictors due to limited number of sample units ($n = 30$ sites).

For each response variable, we ranked all models using the small-sampled Akaike Information Criterion (AICc), and built an average model (Anderson 2008) considering only the parsimonious models (i.e., presenting AICc ≤ 2). However, when the null model was one of the most parsimonious models, we always chose this model because we believe that there is no simpler way to explain a given pattern than through chance. Using the DHARMa package (Hartig 2022), we assessed the model fit and did not detect overdispersion or heteroscedasticity in the parsimonious models. Additionally, we tested spatial autocorrelation in the residuals of each average model using the Moran test (Bivand et al. 2013). All analyses were conducted using the R software (R Core Team 2023).

Results

We recorded 114 species and 8,299 individuals in 30 shaded cocoa agroforest systems. Amphibians emerged as the most diverse group, with 7,283 individuals distributed across 15 families and 74 species, the majority (84%) of which are endemic to Brazil. For reptiles, we recorded 1,016 individuals distributed across 17 families and 40 species, with 12 species being endemic to Brazil. The number of amphibian species recorded across the 30 cocoa agroforests ranged from 9 to 32 species (mean ± standard deviation; 19.63 ± 4.46) and from 120 to 497 individuals (242.77 ± 81.31). In reptiles, the number of species recorded among the 30 agroforests ranged from 3 to 14 (8 ± 2.7) and the number of individuals ranged from 6 to 123 (33.87 ± 27.21).

Our results indicated that several environmental variables were included in the average models used to explain the multiple dimensions of richness and diversity of amphibians and reptiles (Table 1). Additionally, these models showed good fit (Appendix 6), and we did not detect spatial autocorrelation in the residuals of models (Appendix 7).

Our analysis showed that landscape predictors are more important than local factors in determining the multiple dimensions of richness and diversity of amphibians and reptiles (Table 1). For amphibians, we observed that taxonomic richness and diversity, as well as phylogenetic richness, were positively affected by the landscape pasture cover (Fig. 2). We found that functional richness is negatively affected by forest edge density (Fig. 2c). In addition, we observed lower functional richness in the region with high forest cover (Fig. 2d). Our findings also highlighted a negative effect of the number of forest fragments on amphibian functional diversity (Fig. 2e).

For reptiles, we detected a positive effect of landscape forest cover on taxonomic richness and phylogenetic diversity (Fig. 2g and m). Similarly, we observed a positive effect of forest edge density on taxonomic and phylogenetic richness (Fig. 2h and l). Our findings also evidenced that relative humidity positively affects functional richness and diversity (Fig. 2i and k). In contrast, we observed a negative effect of air temperature on reptile functional richness (Fig. 2j).

Finally, we detected that activity time, microhabitat, and reproductive mode were not randomly distributed across the phylogenetic trees of the amphibian and reptile species, indicating a strong phylogenetic signal in these functional traits for both taxonomic groups (see results in Appendix 9).

Table 1. Average models used to assess the effect of the environmental predictors on the taxonomic (^{0}TD, ^{1}TD), functional (^{0}FD, ^{1}FD) and phylogenetic (^{0}PD, ^{1}PD) richness and diversity of amphibians and reptiles. For each landscape variable, we indicated in parentheses the best spatial scale of effect previously identified (see Appendix 1). Significant predictors (P-value < 0.05) are indicated in bold.

	Predictors	Estimate	Standard error	Z-value	P-value
Amphibians					
^{0}TD	**Intercept**	**2.72**	**0.92**	**2.85**	**0.004**
	Pasture cover (1000-m radius)	**0.73**	**0.25**	**2.72**	**0.006**
	Forest edge density (1000-m radius)	-12.49	17.32	0.69	0.49
	Number of shade trees	-0.06	0.08	0.69	0.49
	Number of fallen trunks	0.05	0.07	0.73	0.47
	Air temperature	0.05	0.08	0.67	0.5
^{1}TD	Intercept	1.44	1.22	1.15	0.24
	Pasture cover (400-m radius)	**1.72**	**0.54**	**3.04**	**0.002**
	Number of forest fragments (900-m radius)	-0.01	0.00	1.46	0.144
	Number of understory plants	0.16	0.10	1.57	0.117
	Relative humidity	0.03	0.02	1.32	0.18
^{0}FD	Intercept	0.86	1.49	0.56	0.57
	Pasture cover (800-m radius)	0.12	0.12	0.98	0.33
	Forest edge density (400-m radius)	**-9.09**	**3.97**	**2.20**	**0.03**
	Number of fallen trunks	0.03	0.03	0.99	0.32
	Canopy cover	0.03	0.02	1.29	0.20
	Air temperature	-0.03	0.05	0.96	0.34
	Relative humidity	0.01	0.01	1.48	0.14
	Region: High Agroforest Cover	-0.01	0.04	0.38	0.71
	Region: High Forest Cover	**-0.10**	**0.04**	**2.60**	**0.01**
^{1}FD	**Intercept**	**0.87**	**0.13**	**6.41**	**< 0.001**
	Native forest cover (900-m radius)	-0.21	0.13	1.49	0.14
	Pasture cover (400-m radius)	0.29	0.17	1.64	0.10
	Number of forest fragments (900-m radius)	**-0.005**	**0.002**	**2.22**	**0.03**
	Number of shade trees	-0.05	0.04	1.22	0.22
	Number of fallen trunks	0.03	0.03	0.99	0.32
	Canopy cover	-0.03	0.002	1.07	0.28
^{0}PD	**Intercept**	**7.43**	**0.17**	**42.57**	**< 0.001**
	Native forest cover (800-m radius)	-0.32	0.17	1.83	0.07
	Pasture cover (1000-m radius)	**0.46**	**0.21**	**2.06**	**0.04**
	Forest edge density (1000-m radius)	-19.06	12.69	1.44	0.15
	Number of fallen trunks	0.04	0.05	0.78	0.43
^{1}PD	**Intercept (null model)**	6.3	0.19	327.4	**< 0.001**
Reptiles					
^{0}TD	Intercept	0.57	2.18	0.25	0.8
	Native forest cover (1000-m radius)	**1.11**	**0.51**	**2.12**	**0.03**
	Forest edge density (500-m radius)	**56.29**	**26.33**	**2.05**	**0.04**
	Number of shade trees	0.32	0.32	0.97	0.33
	Number of fallen trunks	-0.25	0.22	1.08	0.28
	Relative humidity	0.04	0.04	1.004	0.31

^{1}TD	Intercept	0.18	2.11	0.01	0.93
	Native forest cover (900-m radius)	0.79	0.41	1.89	0.07
	Forest edge density (500-m radius)	41.54	21.49	1.87	0.06
	Relative humidity	0.03	0.03	1.06	0.3
^{0}FD	Intercept	-3.32	4.39	0.72	0.47
	Native forest cover (800-m radius)	0.59	0.35	1.61	0.11
	Forest edge density (600-m radius)	28.62	16.21	1.68	0.09
	Number of forest fragments (500-m radius)	0.02	0.02	1.33	0.18
	Air temperature	**-0.25**	**0.12**	**2.1**	**0.04**
	Relative humidity	**0.057**	**0.025**	**2.14**	**0.03**
^{1}FD	**Intercept**	**-4.01**	**1.47**	**2.64**	**0.01**
	Forest edge density (700-m radius)	22.36	14.48	1.48	0.14
	Number of forest fragments (500-m radius)	0.01	0.01	0.89	0.37
	Relative humidity	**0.05**	**0.02**	**2.93**	**0.003**
	Region: High Agroforest Cover	-0.14	0.09	1.51	0.13
	Region: High Forest Cover	-0.22	0.12	1.72	0.09
^{0}PD	**Intercept**	**5.07**	**2.12**	**2.33**	**0.02**
	Native forest cover (1000-m radius)	0.72	0.39	1.79	0.07
	Forest edge density (500-m radius)	**38.98**	**19.38**	**1.94**	**0.05**
	Number of shade trees	0.15	0.12	1.15	0.25
	Relative humidity	0.034	0.03	1.25	0.21
^{1}PD	**Intercept**	**4.95**	**1.8**	**2.7**	**0.006**
	Native forest cover (1000-m radius)	**0.53**	**0.26**	**1.99**	**0.04**
	Forest edge density (500-m radius)	21.82	13.99	1.5	0.13
	Number of understory plants	-0.07	0.07	0.91	0.36
	Relative humidity	0.03	0.01	1.45	0.13

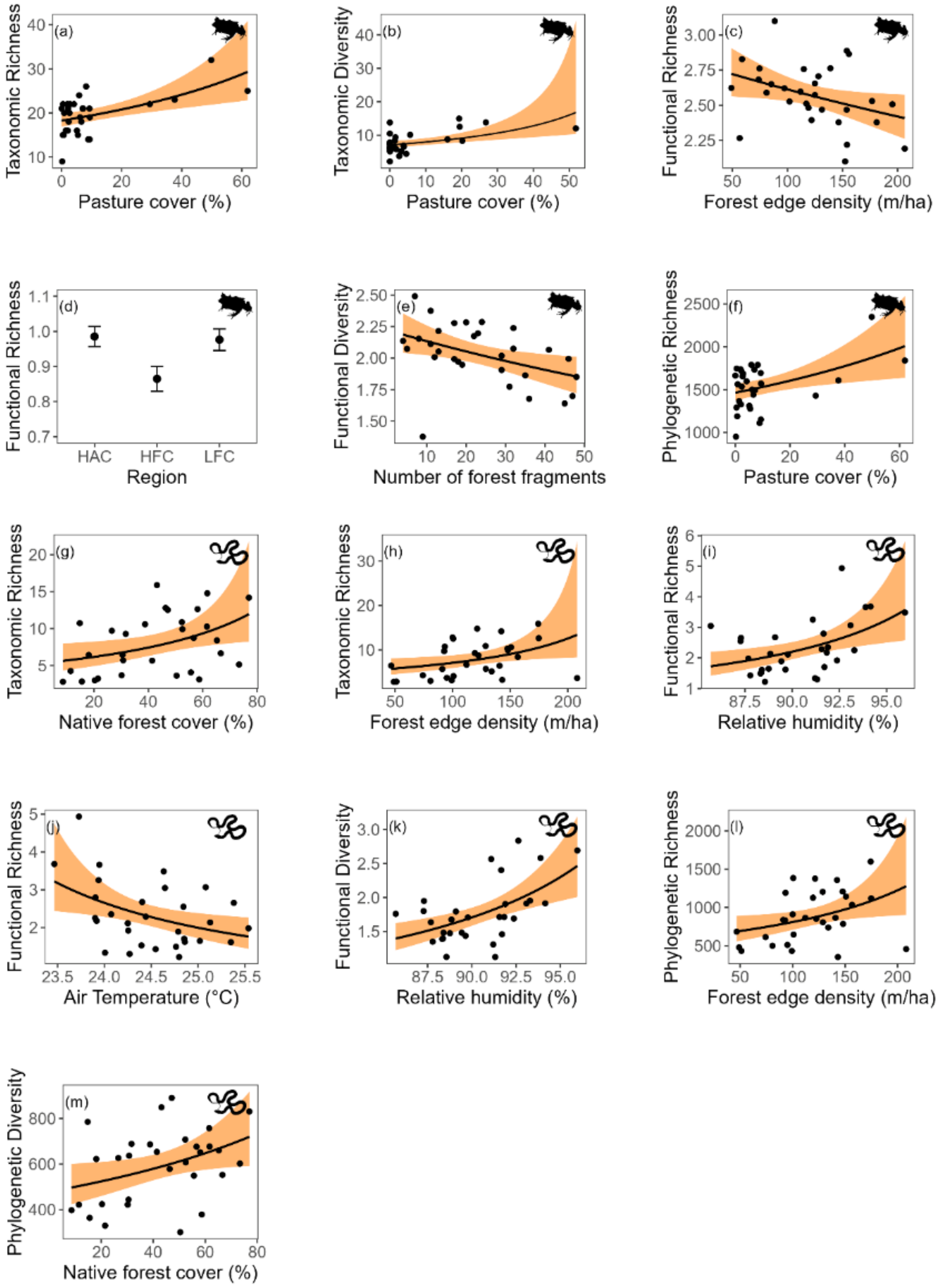

Figure 2. Effect of environmental predictors on multiple dimensions of richness and diversity of the amphibian (a-f) and reptile (g-m) communities recorded in 30 shaded cocoa agroforest systems (black dots). We presented only significant relationships indicated in the average models (Table 1). The orange area represents the 95%

confidence interval.; HAC: High Agroforest Cover region; HFC: High Forest Cover region; LFC: Low Forest Cover region.

Discussion

Our study revealed that landscape predictors are more important than local factors in determining multiple dimensions of the richness and diversity of amphibian and reptile communities in shaded cocoa agroforests. Furthermore, we observed divergent responses between the two groups to environmental changes, with amphibians showing varied responses to changes in landscape structure, while reptiles consistently responded positively to such alterations. In particular, agroforest systems located in landscapes dominated by pasture areas may favor taxonomic richness and diversity, as well as phylogenetic richness of amphibians. In contrast, in landscapes highly fragmented and characterized by high forest edge density, agroforests showed functionally impoverished amphibian communities. For reptiles, we detected that shaded cocoa agroforests in forested landscapes harbor high species richness and diversity. Also, such agroforests present high reptile phylogenetic diversity when located in landscapes dominated by forest edges. Our findings also highlighted that agroforests with high relative humidity can harbor functionally distinct reptile communities. In contrast, increasing local temperature have a negative effect on functional richness of this group. As discussed below, these results have direct implications for the conservation of amphibians and reptiles in human-modified landscapes.

Although we expected richness and diversity of the multiple dimensions of amphibian and reptile communities to be similarly affected by environmental predictors, divergent patterns were detected. For example, in amphibians, forest edge density influenced only functional richness, whereas the number of fragments impacted functional diversity. A similar pattern was observed in reptiles, where forest cover influenced only taxonomic richness and functional diversity, forest edge density impacted only taxonomic and phylogenetic richness, and air temperature affected only functional richness. This divergence could be attributed to the distinct aspects of the community that each index captures. For example, in the order $q = 0$, the indices reflect species richness, ecological traits, or lineages without considering relative abundances, whereas in $q = 1$, the indices account for species abundance and evenness, thereby emphasizing those species, ecological traits, or lineages that are more common within the community (Chao et al. 2021). In this sense, environmental variables, such as forest amount, could promote an increase in the presence of rare species without impacting the relative abundance of species that are more common within the community. Conversely, forest edge density could lead to environmental changes that decrease the amount of certain ecological traits in many amphibians, without affecting those traits that are commonly shared among species. These divergent response between richness and diversity metrics were also observed by Jithin et al. (2023), who found that the conversion of natural rocky outcrops into agroforestry plantations and rice fields reduces microhabitat availability, leading to a decline in the diversity of common and dominant species in the community of amphibians, but did not affect species richness.

Contrary to our predictions, we observed that landscape pasture cover has a positive effect on amphibian richness and diversity, and phylogenetic richness. This result is surprising given that pasture areas are hostile environments for amphibian species, due to their high temperatures and high concentrations of agrochemicals, as well as low availability of microhabitats, making species more exposed to predators and parasites (McKenzie 2007; Becker et al. 2010; López-Bedoya et al. 2022). These characteristics create harsh environmental filters, allowing only a reduced number of species, usually phylogenetically related ones, to survive in pasture-dominated landscapes (Pineda and Halffter 2004; Urbina-Cardona et al. 2006; Lara-Tufiño et al. 2019). However, our result may be associated with the crowding effect (Vallejos et al. 2020). In deforested landscapes dominated by pastures, species are forced to move to the few friendly environments, such as cocoa agroforests, to obtain necessary resources for their survival (Grez et al. 2004; Vallejos et al. 2020). This can result in increased population density, potentially creating more diverse communities than before the disturbance (Grez et al. 2004). Also, the crowding effect may be accentuated by the disappearance of predators in degraded landscapes (Cudney-Valenzuela et al. 2023), thus relaxing predation pressure on amphibian populations. Furthermore, we recorded several amphibian species that show low sensitivity to disturbances and therefore high adaptability to survive in anthropogenic areas. For example, *Adenomera thomei*, *Boana atlantica*, *B. semilineata*, *Leptodactylus mystaceus*, *Pithecopus rohdei*, *Pristimantis paulodutrai*, *Rhinella crucifer*, *Ololygon argyreornata*, are species widely observed in disturbed habitats such as secondary forests, forest edges (Almeida-Gomes et al. 2019; IUCN 2022), and were commonly recorded in the cocoa agroforests. Such species can obtain resources from additional habitats, including artificial ponds, in the pasture areas adjacent to agroforests (da Silva et al. 2011; Oda et al. 2016).

Our results also revealed that change in landscape configuration can negatively impact the functional richness and diversity of amphibians in cocoa agroforests. In particular, we detected that agroforests located in fragmented landscapes dominated by forest edges harbor functionally impoverished amphibian communities. In such landscapes, microclimatic changes resulting from edge effects can be more intense and act as an ecological filter (Isaacs and Urbina-Cardona 2011; Zabala-Forero and Urbina-Cardona 2021), selecting only a few species with specific ecological traits capable of tolerating such disturbances (Álvarez-Grzybowska et al. 2020; Posse-Sarmiento and Banks-Leite 2024). Indeed, several studies have reported that increased forest edge density in the landscape can reduce the presence of amphibian species sensitive to forest fragmentation (Urbina-Cardona et al. 2006; Schneider-Maunoury et al. 2016) and promote a proliferation of disturbance-adapted species (Schneider-Maunoury et al. 2016; Posse-Sarmiento and Banks-Leite 2024). These species share similar ecological traits, such as large-bodied size, or a pond-breeding mode, which favor their occurrence in fragmented landscapes (Mendenhall et al. 2014; Hernández-Ordóñez et al. 2019; Ríos-Orjuela et al. 2024). Furthermore, as forest fragmentation increases, there is a simultaneous reduction in fragment size and an increase in isolation between them (Fahrig 2013). Under this scenario, native species may not obtain sufficient resources for their survival in small fragments, thus being forced to disperse across the landscape to find supplementary habitats (Faria et al. 2007; Becker et al. 2010; Almeida-Gomes et al. 2016). However, only species sharing similar ecological traits associated with high vagility could colonize new habitats, such as agroforests (Zabala-Forero and Urbina-Cardona 2021; Ríos-Orjuela et al. 2024). Therefore, the intensified edge effect in small fragments along with greater isolation between them can be crucial factors in the reduction of amphibian functional diversity in cocoa agroforests located in highly fragmented landscapes.

Our study also demonstrated that agroforests located within the more forested region exhibit lower functional richness of amphibians. In highly forested regions, amphibian species obtain necessary resources in their native habitat, thus only a limited number of species sharing specific ecological traits, typically habitat-generalist species, will colonize human-modified environments (Almeida-Gomes et al. 2019; Vega-Agavo et al. 2021). Conversely, in regions with limited native habitat, less intensive agricultural systems like shaded cocoa agroforests can serve as supplementary habitat for many species, including amphibians (Faria et al. 2007; Wanger et al. 2010;

Cervantes-López et al. 2022). This is an intriguing result as it demonstrates that the conservation value of agroforests also depends on the amount of native habitat at the regional scale.

For reptiles, we observed that increased forest cover in the landscape positively impacts taxonomic richness and phylogenetic diversity in cocoa agroforests. These findings are consistent with previous studies that identified a diverse reptile community in agroforestry systems located in more forested landscapes (Faria et al. 2007; Vega-Agavo et al. 2021; Cervantes-López and Morante-Filho 2024). Similar results were also observed in recent studies conducted in fragmented landscapes in Brazil, where increased forest cover positively affected snake species richness and favored the phylogenetic diversity of these reptiles (Rincón-Aranguri et al. 2023; Leal-Santos et al. 2024). Our findings are also supported by the Habitat Amount Hypothesis, which posits that species richness depends on the amount of habitat available in the landscape (Fahrig 2013). In particular, forested landscapes can provide a wide range of essential resources for the coexistence of phylogenetically distinct species. Additionally, such landscapes exhibit greater connectivity among remnant habitats (Tscharntke et al. 2012), facilitating species dispersal and thus species exchange between native forests and agroforests (see spillover effect, Dunning et al. 1992).

Our findings highlighted that forest edge density positively impacts reptile richness, leading to phylogenetically distinct communities in agroforests. In particular, forest edges can increase abiotic heterogeneity as well as the availability of resources and microhabitats for some species, including reptiles (Murcia 1995; Pfeifer et al. 2017). For example, several studies have reported that forest edges can provide shelters, such as fallen logs and dense vegetation, which are used as hiding sites, foraging or breeding sites for many species and assist in reducing ecotapariste infections (Schlaepfer and Gavin 2001; Hansen et al. 2019). Another relevant point is that forest edges can act as dispersal areas for species between different environments within landscapes (Murcia 1995; Fahrig 2017). Therefore, edges can facilitate the colonization of agroforests by different species, creating rich communities of reptiles, including species from different phylogenetic clades. In fact, the colonization of species from the matrix to the forest edges is a pattern observed in studies with tropical amphibians (Posse-Sarmiento and Banks-Leite 2024), mammals (Santos-Filho et al. 2008), and reptiles (Cabrera-Guzmán and Reynoso 2012; Carvajal-Cogollo and Urbina-Cardona 2015). These studies showed that a high proportion of species living in the matrix can also be found in forests and vice versa. In particular, some of the recorded species in the cocoa agroforests that may inhabit forest edges are lizards *Ameiva ameiva*, *Anolis punctatus*, *Leposoma scincoides*, *Polychrus marmoratus*, *Tropidurus torquatus*, and *Salvator merianae*, as well as the snakes *Bothrops leucurus*, *Chironius exoletus*, *Corallus hortulanus*, and *Xenopholis scalaris*.

Surprisingly, in our study, only two local factors influenced the reptile community. Specifically, we observed that increased relative humidity positively impacted richness and functional diversity, while increased temperature negatively affected functional richness. Similar results have been observed in studies conducted in different environments, including coffee agroforestry systems (Ríos-Orjuela et al. 2024), live fences (Pérez-García 2023), and tropical forest fragments (Cabrera-Guzmán and Reynoso 2012). In particular, an increase in temperature can lead to thermal stress in many species, thereby increasing mortality in embryos and juveniles, as well as directly affecting growth rates (Raynal et al. 2022). Therefore, changes in temperature and humidity act as an important ecological filter, selecting species with specific ecological traits capable of withstanding such disturbances (Daltry et al. 1998; Galliard et al. 2021). For example, some studies have demonstrated that increasing temperatures in agricultural areas may limit the presence of reptiles with certain ecological traits, including species with small body size, diurnal activity, and oviparous reproductive mode (Carvajal-Cogollo and Urbina-Cardona 2015). In contrast, environments with high humidity, such as shaded agroforestry systems, may provide suitable microhabitats for the reproductive (Sales et al. 2020) and thermal needs of reptiles (Macip-Ríos and Muñoz 2008), thereby reducing health issues associated with dysclysis and aphagia (Daltry et al. 1998). Therefore, cocoa agroforests presenting moderate temperature and high humidity provide microclimatic conditions favorable for the survival and reproduction of reptile species with diverse ecological needs.

In summary, our findings revealed that the taxonomic and phylogenetic dimensions of both groups showed similar responses to the environmental predictors evaluated, while the functional dimension exhibited a distinct response. For example, the taxonomic and phylogenetic diversity of amphibians were affected by changes in landscape composition, particularly the amount of pasture, while the richness and functional diversity of this group responded to changes in landscape configuration (i.e., number of forest fragments and edge density). For reptiles, while we detected that taxonomic richness and phylogenetic diversity were affected by forest cover, and taxonomic and phylogenetic richness by edge density, functional metrics only responded to changes in abiotic conditions (temperature and humidity). These divergent results between functional metrics and the other dimensions of diversity may be associated with the functional redundancy within communities, where distinct species share similar traits and ecological roles (Fetzer et al. 2015). In this scenario, the loss of certain species may decrease taxonomic and phylogenetic diversity without affecting functional diversity (Edie et al. 2018). Additionally, it is expected that phylogenetically related species present similar responses to environmental stressors (Wiens and Graham 2005), showing high phylogenetic signal in the ecological traits, as observed in our study. This strong signal suggests that traits such as activity patterns, microhabitat use or reproductive mode may influence the ability of species to colonize or inhabit cocoa agroforests. For example, in cocoa agroforests systems, the preservation of structural characteristics similar to those of forests, such as tree shade, reduces water evaporation (Teixeira et al. 2015), helping to maintain water pools that support a wide variety of species relying on aquatic habitats, semi-aquaitc or water bodies for reproduction. In this way, land-use change can act as a strong filter that selects phylogenetically related species with similar characteristics, which are likely adapted to disturbances (Nowakowski et al. 2018). These results highlighted the importance of evaluating multiple dimensions of species diversity (Cadotte and Tucker 2018), as such dimensions may respond differently to environmental disturbances.

Conclusion

Given the high rates of deforestation, especially in tropical forests, there is an urgent need to develop strategies for conserving native species in human-modified landscapes (Arroyo-Rodríguez et al. 2020). While many conservationists advocate for the restoration of degraded areas, others also support the use of agricultural systems capable of reconciling production with biodiversity conservation (Green et al. 2005; Phalan et al. 2011). In this sense, agroforest systems emerge as a key element in safeguarding native species (Perfecto and Vandermeer 2010). However, our study revealed that the conservation value of shaded cocoa agroforests depends especially on the landscape context in which these agricultural systems are located. Furthermore, we also highlighted that amphibian and reptile species show divergent responses to changes in landscape structure.

Our findings revealed that in pasture-dominated landscapes, cocoa agroforests systems can serve as refuges for amphibian species, thereby hosting rich species communities composed of phylogenetically distinct species. Although this is an interesting result, caution is needed in its interpretation as it is uncertain whether species can be maintained in the long term due to the pervasive effects of pasture (López-Bedoya et al. 2022). We also found that in less fragmented landscapes, i.e., those with fewer forest fragments and edges, agroforests can host amphibian species with diverse functional traits. Therefore, management strategies designed to decrease fragmentation, including the creation of forest corridors to connect isolated fragments (Arroyo-Rodríguez et al. 2020), may help in maintaining or even increasing the functional diversity of amphibians in such agroforests.

For reptiles, agroforests located in highly forested landscapes, including those with a high number of forest edges, support communities with high species richness and phylogenetic diversity. Therefore, forest restoration in severely deforested regions is a crucial measure for the conservation of reptile species in agricultural landscapes (Arroyo-Rodriguez et al. 2020). Importantly, our results revealed that the climatic conditions of cocoa agroforests are crucial for maintaining the functional diversity of reptiles. Although our study did not detect a direct effect of local vegetation characteristics, we believe that maintaining multilayered agroforests (i.e., those with a diversity of trees and a closed canopy) can reduce solar incidence in the understory (Macip-Ríos and Muñoz-Alonso 2008). This aspect may contribute to maintaining temperature and increasing humidity, thus allowing the presence of reptile species with distinct ecological traits in these agricultural systems.

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Competing Interests

All authors of this manuscript declare that there is no conflict of interest.

Author contributions

M.J. Cervantes-Lopez coordinated field sampling, collected data, wrote funding applications, drafted the manuscript, created databases, and performed analyses. G. Alves-Ferreira contributed significantly to field sampling, assisted with data entry, performed analyses, created and refined figures, and revised the final manuscript. J.C. Morante-Filho supervised all stages of the study, helped secure funding, and reviewed all versions of the manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethical approval

The license for the management, capture, image recording and the collection of some of the individuals of amphibians and reptiles observed in this study was approved by the Comissão De Ética No Uso De Animais Da Universidade Estadual De Santa Cruz (CEUA/UESC) (protocol number 038/21) and authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (IBAMA) through the Sistema de Autorização e Informação em Biodiversidade (SISBIO, license number 81341-1).

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Supporting information

Appendix 1. Landscape scale effect

Considering that the effect of landscape variables on biodiversity depends on the spatial scale at which predictors are measured (i.e. the so-called "scale of landscape effects"; sensu Fahrig 2013; Jackson and Fahrig 2015), we estimated native forest cover, pasture cover, forest edge density and number of forest fragments within seven different-sized buffers (i.e., landscapes), ranging from 400- to 1000-m radius. Thus, we obtained landscapes of 50.24 ha (400 m), 78.50 ha (500 m), 113.04 ha (600 m), 153.86 ha (700 m), 200.96 ha (800 m), 254.34 ha (900 m) and 314 ha (1000 m). We used Linear Models to identify the landscape size most appropriate to analyze the effect of each landscape variable on each response variable. Following Fahrig (2013) and Jackson and Fahrig (2015), the scale of effect of each landscape predictor was simply defined as the landscape size in which the landscape-response relationship was strongest (i.e., with the highest R^2).

Table S1. Results of associations between landscape metrics and multiple dimensions of amphibian and reptile richness and diversity in different landscape sizes (buffers). The size of the scale with the highest effect (i.e., highest determination coefficient – R^2) is indicated in bold.

Response variable	**Landscape metric**	**Buffer size (m)**	**Amphibians**		**Reptiles**	
			R^2	**p-value**	**R^2**	**p-value**
Species richness	Native forest cover	400	0.10	0.09	0.08	0.13
Species richness	Native forest cover	500	0.11	0.07	0.11	0.08
Species richness	Native forest cover	600	0.13	0.05	0.13	0.05
Species richness	Native forest cover	700	0.15	0.04	0.15	0.04
Species richness	Native forest cover	**800**	**0.16**	**0.03**	0.16	0.03
Species richness	Native forest cover	900	0.15	0.03	0.17	0.02
Species richness	Native forest cover	**1000**	0.15	0.04	**0.17**	**0.02**
Species diversity	Native forest cover	**400**	**0.03**	**0.38**	0.09	0.12
Species diversity	Native forest cover	500	0.02	0.45	0.11	0.08
Species diversity	Native forest cover	600	0.01	0.54	0.12	0.06
Species diversity	Native forest cover	700	0.01	0.58	0.12	0.06
Species diversity	Native forest cover	800	0.01	0.63	0.13	0.05

Species diversity	Native forest cover	**900**	0.01	0.65	**0.14**	**0.04**
Species diversity	Native forest cover	1000	0.01	0.67	0.14	0.04
Functional richness	Native forest cover	400	0.01	0.59	0.04	0.30
Functional richness	Native forest cover	500	0.01	0.53	0.05	0.25
Functional richness	Native forest cover	600	0.02	0.46	0.06	0.21
Functional richness	Native forest cover	700	0.03	0.39	0.07	0.17
Functional richness	Native forest cover	**800**	0.03	0.36	**0.07**	**0.16**
Functional richness	Native forest cover	900	0.03	0.36	0.07	0.16
Functional richness	Native forest cover	**1000**	**0.03**	**0.35**	0.07	0.17
Functional diversity	Native forest cover	400	0.00	0.89	0.01	0.53
Functional diversity	Native forest cover	500	0.00	0.83	0.01	0.52
Functional diversity	Native forest cover	600	0.00	0.76	0.01	0.52
Functional diversity	Native forest cover	700	0.00	0.73	0.02	0.48
Functional diversity	Native forest cover	**800**	0.01	0.69	**0.02**	**0.45**
Functional diversity	Native forest cover	**900**	**0.01**	**0.67**	0.02	0.48
Functional diversity	Native forest cover	1000	0.01	0.68	0.02	0.51
Phylogenetic richness	Native forest cover	400	0.10	0.10	0.06	0.20
Phylogenetic richness	Native forest cover	500	0.11	0.07	0.08	0.12
Phylogenetic richness	Native forest cover	600	0.13	0.05	0.11	0.08

Phylogenetic richness	Native forest cover	700	0.15	0.03	0.12	0.06
Phylogenetic richness	Native forest cover	**800**	**0.16**	**0.03**	0.13	0.05
Phylogenetic richness	Native forest cover	900	0.16	0.03	0.15	0.04
Phylogenetic richness	Native forest cover	**100**0	0.16	0.03	**0.16**	**0.03**
Phylogenetic diversity	Native forest cover	**400**	**0.02**	**0.45**	0.06	0.18
Phylogenetic diversity	Native forest cover	500	0.02	0.49	0.08	0.12
Phylogenetic diversity	Native forest cover	600	0.01	0.56	0.11	0.09
Phylogenetic diversity	Native forest cover	700	0.01	0.57	0.12	0.07
Phylogenetic diversity	Native forest cover	800	0.01	0.58	0.13	0.05
Phylogenetic diversity	Native forest cover	900	0.01	0.57	0.15	0.04
Phylogenetic diversity	Native forest cover	**1000**	0.01	0.58	**0.16**	**0.03**
Species richness	Pastures cover	400	0.20	0.01	0.01	0.52
Species richness	Pastures cover	**500**	0.18	0.02	**0.02**	**0.42**
Species richness	Pastures cover	600	0.22	0.01	0.01	0.53
Species richness	Pastures cover	700	0.27	0.00	0.01	0.66
Species richness	Pastures cover	800	0.29	0.001	0.01	0.71
Species richness	Pastures cover	900	0.31	0.001	0.00	0.77
Species richness	Pastures cover	**1000**	**0.31**	**0.001**	0.00	0.77
Species diversity	Pastures cover	**400**	**0.33**	**0.0008**	0.00	0.73
Species diversity	Pastures cover	**500**	0.28	0.002	**0.01**	**0.59**
Species diversity	Pastures cover	600	0.30	0.001	0.00	0.73
Species diversity	Pastures cover	700	0.32	0.001	0.00	0.91
Species diversity	Pastures cover	800	0.31	0.001	0.00	0.94
Species diversity	Pastures cover	900	0.31	0.001	0.00	0.98
Species diversity	Pastures cover	1000	0.32	0.001	0.00	0.98

Functional richness	Pastures cover	400	0.09	0.11	0.01	0.67
Functional richness	Pastures cover	**500**	0.07	0.15	**0.01**	**0.55**
Functional richness	Pastures cover	600	0.08	0.12	0.01	0.63
Functional richness	Pastures cover	700	0.10	0.08	0.00	0.79
Functional richness	Pastures cover	**800**	**0.12**	**0.07**	0.00	0.87
Functional richness	Pastures cover	900	0.11	0.07	0.00	0.96
Functional richness	Pastures cover	1000	0.11	0.07	0.00	0.98
Functional diversity	Pastures cover	**400**	**0.10**	**0.09**	0.00	0.76
Functional diversity	Pastures cover	**500**	0.08	0.13	**0.01**	**0.63**
Functional diversity	Pastures cover	600	0.08	0.12	0.00	0.72
Functional diversity	Pastures cover	700	0.08	0.13	0.00	0.91
Functional diversity	Pastures cover	800	0.06	0.17	0.00	1.00
Functional diversity	Pastures cover	900	0.06	0.20	0.00	0.93
Functional diversity	Pastures cover	1000	0.06	0.20	0.00	0.89
Phylogenetic richness	Pastures cover	400	0.12	0.06	0.02	0.41
Phylogenetic richness	Pastures cover	**500**	0.10	0.08	**0.03**	**0.35**
Phylogenetic richness	Pastures cover	600	0.12	0.06	0.02	0.45
Phylogenetic richness	Pastures cover	700	0.16	0.03	0.01	0.59

Phylogenetic richness	Pastures cover	800	0.19	0.02	0.01	0.61
Phylogenetic richness	Pastures cover	900	0.20	0.01	0.01	0.62
Phylogenetic richness	Pastures cover	**1000**	**0.21**	**0.01**	0.01	0.60
Phylogenetic diversity	Pastures cover	**400**	**0.14**	**0.04**	0.02	0.48
Phylogenetic diversity	Pastures cover	**500**	0.11	0.07	**0.03**	**0.40**
Phylogenetic diversity	Pastures cover	600	0.12	0.06	0.02	0.49
Phylogenetic diversity	Pastures cover	700	0.13	0.05	0.01	0.60
Phylogenetic diversity	Pastures cover	800	0.12	0.06	0.01	0.62
Phylogenetic diversity	Pastures cover	900	0.12	0.06	0.01	0.63
Phylogenetic diversity	Pastures cover	1000	0.13	0.05	0.01	0.61
Species richness	Forest edge density	400	0.08	0.12	0.09	0.10
Species richness	Forest edge density	**500**	0.06	0.20	**0.15**	**0.03**
Species richness	Forest edge density	600	0.06	0.19	0.15	0.04
Species richness	Forest edge density	700	0.10	0.09	0.10	0.08
Species richness	Forest edge density	800	0.11	0.08	0.08	0.13
Species richness	Forest edge density	900	0.12	0.06	0.06	0.18
Species richness	Forest edge density	**1000**	**0.14**	**0.04**	0.06	0.18
Species diversity	Forest edge density	**400**	**0.12**	**0.07**	0.07	0.15
Species diversity	Forest edge density	**500**	0.06	0.19	**0.12**	**0.06**
Species diversity	Forest edge density	600	0.06	0.19	0.12	0.06
Species diversity	Forest edge density	700	0.10	0.09	0.09	0.11
Species diversity	Forest edge density	800	0.09	0.10	0.07	0.14
Species diversity	Forest edge density	900	0.09	0.11	0.06	0.20
Species diversity	Forest edge density	1000	0.08	0.13	0.05	0.22
Functional	Forest edge density	**400**	**0.14**	**0.04**	0.05	0.25

richness						
Functional richness	Forest edge density	500	0.09	0.11	0.09	0.11
Functional richness	Forest edge density	**600**	0.07	0.17	**0.10**	**0.09**
Functional richness	Forest edge density	700	0.10	0.08	0.10	0.09
Functional richness	Forest edge density	800	0.12	0.07	0.08	0.13
Functional richness	Forest edge density	900	0.13	0.05	0.06	0.19
Functional richness	Forest edge density	1000	0.13	0.05	0.06	0.20
Functional diversity	Forest edge density	400	0.00	0.89	0.02	0.45
Functional diversity	Forest edge density	500	0.00	0.83	0.05	0.23
Functional diversity	Forest edge density	600	0.00	0.76	0.07	0.16
Functional diversity	Forest edge density	**700**	0.00	0.73	**0.09**	**0.12**
Functional diversity	Forest edge density	800	0.01	0.69	0.07	0.16
Functional diversity	Forest edge density	**900**	**0.01**	**0.67**	0.05	0.23
Functional diversity	Forest edge density	1000	0.01	0.68	0.05	0.23
Phylogenetic richness	Forest edge density	400	0.11	0.07	0.10	0.09
Phylogenetic richness	Forest edge density	**500**	0.08	0.13	**0.14**	**0.04**
Phylogenetic richness	Forest edge density	600	0.07	0.15	0.13	0.05
Phylogenetic richness	Forest edge density	700	0.11	0.07	0.09	0.11
Phylogenetic richness	Forest edge density	800	0.13	0.05	0.07	0.16

Phylogenetic richness	Forest edge density	900	0.14	0.04	0.06	0.19
Phylogenetic richness	Forest edge density	**1000**	**0.15**	**0.03**	0.06	0.20
Phylogenetic diversity	Forest edge density	**400**	**0.11**	**0.07**	0.07	0.16
Phylogenetic diversity	Forest edge density	**500**	0.06	0.19	**0.10**	**0.10**
Phylogenetic diversity	Forest edge density	600	0.05	0.23	0.09	0.11
Phylogenetic diversity	Forest edge density	700	0.10	0.09	0.07	0.16
Phylogenetic diversity	Forest edge density	800	0.10	0.09	0.06	0.19
Phylogenetic diversity	Forest edge density	900	0.10	0.10	0.05	0.24
Phylogenetic diversity	Forest edge density	1000	0.09	0.11	0.05	0.25
Species richness	Number of forest fragments	400	0.00	0.84	0.02	0.47
Species richness	Number of forest fragments	**500**	**0.05**	**0.25**	0.00	0.88
Species richness	Number of forest fragments	600	0.03	0.33	0.04	0.31
Species richness	Number of forest fragments	700	0.02	0.44	0.04	0.32
Species richness	Number of forest fragments	800	0.03	0.36	0.06	0.21
Species richness	Number of forest fragments	**900**	0.02	0.49	**0.07**	**0.15**
Species richness	Number of forest fragments	1000	0.01	0.66	0.06	0.18
Species diversity	Number of forest fragments	400	0.02	0.47	0.02	0.45
Species diversity	Number of forest fragments	500	0.00	0.82	0.00	0.88

Species diversity	Number of forest fragments	600	0.03	0.40	0.04	0.31
Species diversity	Number of forest fragments	700	0.04	0.30	0.03	0.38
Species diversity	Number of forest fragments	800	0.05	0.23	0.05	0.24
Species diversity	Number of forest fragments	**900**	**0.07**	**0.15**	**0.06**	**0.18**
Species diversity	Number of forest fragments	1000	0.06	0.20	0.05	0.23
Functional richness	Number of forest fragments	**400**	**0.01**	**0.52**	0.00	0.90
Functional richness	Number of forest fragments	**500**	0.00	0.90	**0.01**	**0.67**
Functional richness	Number of forest fragments	600	0.00	0.83	0.00	0.86
Functional richness	Number of forest fragments	700	0.00	0.78	0.00	1.00
Functional richness	Number of forest fragments	800	0.00	0.81	0.00	0.76
Functional richness	Number of forest fragments	900	0.01	0.67	0.00	0.87
Functional richness	Number of forest fragments	1000	0.01	0.60	0.00	0.97
Functional diversity	Number of forest fragments	400	0.11	0.07	0.00	0.72
Functional diversity	Number of forest fragments	**500**	0.06	0.19	**0.03**	**0.39**
Functional diversity	Number of forest fragments	600	0.12	0.06	0.01	0.59
Functional diversity	Number of forest fragments	700	0.13	0.05	0.02	0.50
Functional diversity	Number of forest fragments	800	0.11	0.07	0.00	0.76
Functional diversity	Number of forest fragments	**900**	**0.18**	**0.02**	0.01	0.66
Functional	Number of forest	1000	0.15	0.04	0.02	0.43

diversity	fragments					
Phylogenetic richness	Number of forest fragments	400	0.00	0.94	0.00	0.84
Phylogenetic richness	Number of forest fragments	**500**	**0.05**	**0.22**	0.00	0.89
Phylogenetic richness	Number of forest fragments	600	0.05	0.24	0.03	0.40
Phylogenetic richness	Number of forest fragments	700	0.02	0.41	0.02	0.47
Phylogenetic richness	Number of forest fragments	800	0.03	0.36	0.03	0.37
Phylogenetic richness	Number of forest fragments	900	0.02	0.41	0.05	0.22
Phylogenetic richness	Number of forest fragments	**1000**	0.01	0.59	**0.06**	**0.20**
Phylogenetic diversity	Number of forest fragments	400	0.05	0.25	0.00	0.94
Phylogenetic diversity	Number of forest fragments	500	0.01	0.64	0.00	0.91
Phylogenetic diversity	Number of forest fragments	600	0.05	0.25	0.02	0.48
Phylogenetic diversity	Number of forest fragments	700	0.05	0.25	0.01	0.59
Phylogenetic diversity	Number of forest fragments	800	0.05	0.22	0.03	0.40
Phylogenetic diversity	Number of forest fragments	**900**	**0.07**	**0.16**	**0.05**	**0.26**
Phylogenetic diversity	Number of forest fragments	1000	0.06	0.19	0.04	0.28

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Appendix 2. Ecological traits of amphibian and reptile species.

Table S2. List of ecological traits used to calculate the functional richness and diversity of amphibian and reptile communities recorded in 30 shaded cocoa agroforest systems.

Trait type	**Ecological trait**	**Atribute**	**Description**	**Funcional meaning**	**Reference**
Numerical	Body length	Trait value in millimeters	It is described as the distance in millimeters from the front end of the snout to the rear edge of the cloaca for anurans. For Caudata and reptiles, it was considered total length.	Associated with nutrient recycling and energy flow through food chains, either as predator or prey.	(Hernández-Ordóñez et al. 2019; Alves-Ferreira et al. 2022)
Numerical	Biomass	Maximum body mass in grams	The amount of biological matter present in organisms measured by the weight of the organism.	A trait linked to the energy stored in the ecosystem, crucial for energy flow due to ecophysiological traits, the diversity of prey, and the quantity of food consumed.	(Cortés-Gómez et al. 2016; Gómez–Ortiz and Moreno 2017; Zabala-Forero and Urbina-Cardona 2021)
Categorical	Activity time	Diurnal; nocturnal; diurnal-nocturnal	The period of the day during which individuals engage in activities such as foraging, singing, among others .	This trait can be related to the types of prey and predators that interact with the organism. Also, it can be related to the balance of matter and differential energy over time.	(Cortés-Gómez et al. 2016; Hernández-Ordóñez et al. 2019)
Categorical	Microhabitat	Fossorial; terrestrial; aquatic; arboreal; semi-arboreal and semi-aquatic	Vertical foraging stratum which the species is predominantly	Trait associated with the extent of potential resources that species can use in the environment. It is also related to	(Cortes et al. 2015; Cortés-Gómez et al.

			associated.	nutrient cycling, the flow of energy through food chains as predatory prey.	2016)
Categorical	Reproductive mode	For amphibians: eggs in water and larval development in water; eggs in vegetation and larval development in water; terrestrial eggs with indirect development in foam; terrestrial eggs with direct development For reptiles: oviparous and viviparous	Reproductive mode refers to the different strategies used by species to reproduce and ensure the survival of their offspring.	This trait is related to the differential energy balance for the production of offspring, as well as to the flow of energy through food chains as predator and prey.	(Cortés-Gómez et al. 2016; Almeida-Gomes et al. 2019; Álvarez-Grzybowska et al. 2020)

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Appendix 3. Species richness and abundance recorded in 30 shaded cocoa agroforest systems.

Table S3. Abundance and species richness of amphibian and reptile species recorded in the 30 shaded cocoa agroforest systems in three regions presenting different land use contexts. We also presenting sample coverage of each agroforest. HAC: High Agroforest Forest Cover region; HFC: High Forest Cover region; LFC: Low Forest Cover region.

Region	Code site	Amphibians			Reptiles		
		Abundance	Species richness	Sample coverage	Abundance	Species richness	Sample coverage
HAC	I10	196	22	0.97	46	14	0.83
HAC	I11	184	20	0.95	43	7	0.95
HAC	I12	232	21	0.96	52	10	0.94
HAC	I13	120	21	0.95	24	7	0.92
HAC	I14	331	19	0.98	47	13	0.87
HAC	I15	352	24	0.99	46	14	0.85
HAC	I16	293	15	0.99	55	11	0.89
HAC	I17	280	22	0.97	25	9	0.80
HAC	I4	226	18	0.98	21	6	0.82
HAC	I8	497	18	0.99	32	6	0.97
HFC	U1	254	14	0.99	13	4	0.86
HFC	U11	263	21	0.97	20	8	0.76
HFC	U12	173	15	0.95	11	6	0.66
HFC	U13	273	26	0.96	6	3	0.76
HFC	U14	208	9	0.99	19	6	0.96
HFC	U15	144	20	0.94	18	8	0.67
HFC	U16	274	14	0.98	12	5	0.77
HFC	U17	146	16	0.97	15	8	0.61
HFC	U3	269	15	1.00	26	9	0.77
HFC	U7	231	22	0.97	20	8	0.81
LFC	B13	139	21	0.96	11	6	0.65
LFC	B14	174	22	0.96	37	11	0.87

LFC	B15	174	16	0.97	123	9	0.98
LFC	B16	385	22	0.99	17	8	0.77
LFC	B18	272	16	0.98	27	5	0.93
LFC	B19	266	21	0.96	69	7	0.96
LFC	B20	239	19	0.98	110	9	0.97
LFC	B21	251	25	0.98	34	6	0.91
LFC	B7	292	32	0.97	20	9	0.76
LFC	B9	145	23	0.95	17	8	0.71

Appendix 4. Pearson correlations between environmental predictors.

Table S4. Pearson correlation values between pairs of environmental predictors used in the statistical analyses. We present the values for each response variable due to the different spatial scales used to calculate landscape metrics (see Table S1)**.** Environmental predictors are presented as: REG (region), FC (Native forest cover), PC (pasture cover), ED (Forest edge density), NFF (Number of forest fragments), NCT (number of cocoa trees), NST (number of shade trees), NFT (number of fallen trunks), NPU (number understory plants), LFD (leaf litter depth), CC (canopy cover), AT (air temperature) and RH (relative humidity). High correlation values (r ≥ 0.70) are indicated in bold.

Amphibians													
Taxonomic richness													
	REG	FC (800m)	PC (1000m)	ED (1000m)	NFF (500m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (800m)	0.42	1											
PC (1000m)	-0.48	-0.42	1										
ED (1000m)	0.48	0.43	-0.44	1									
NFF(500m)	0	-0.49	0.27	0.18	1								
NCT	0.14	-0.05	-0.30	0.03	-0.25	1							
NST	0.29	0.47	-0.10	-0.06	-0.38	0.17	1						
NFT	0.06	0.07	-0.07	-0.10	-0.16	0.35	0.27	1					
NPU	-0.25	0.08	0.22	-0.13	-0.16	0.004	0.20	0.09	1				
LFD	**0.80**	0.44	-0.46	0.38	-0.12	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.28	-0.09	0.18	0.20	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.25	0.13	-0.39	-0.02	-0.03	0.00007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.09	-0.11	0.12	-0.001	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Taxonomic diversity													
	REG	FC (400m)	PC (400m)	ED (400m)	NFF (900m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (400m)	0.32	1											

PC (400m)	-0.49	-0.42	1										
ED (400m)	0.65	0.61	-0.45	1									
NFF (900m)	-0.06	-0.56	-0.05	-0.15	1								
NCT	0.14	-0.13	-0.08	-0.22	-0.18	1							
NST	0.29	0.40	-0.17	0.16	-0.48	0.17	1						
NFT	0.06	-0.01	-0.05	-0.12	-0.23	0.35	0.27	1					
NPU	-0.25	-0.03	0.28	-0.25	-0.31	0.004	0.20	0.09	1				
LFD	**0.80**	0.27	-0.35	0.45	-0.30	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.33	-0.35	0.39	0.11	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.16	0.07	-0.25	-0.03	-0.03	0.00007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.05	-0.18	0.08	0.02	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Functional richness													
	REG	FC (1000m)	PC (800m)	ED (400m)	NFF (400m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (1000m)	0.44	1											
PC (800m)	-0.49	-0.41	1										
ED (400m)	0.65	0.59	-0.36	1									
NFF (400 m)	0.07	-0.43	0.20	0.12	1								
NCT	0.14	-0.02	-0.28	-0.22	-0.07	1							
NST	0.29	0.46	-0.13	0.16	-0.11	0.17	1						
NFT	0.06	0.10	-0.06	-0.12	0.03	0.35	0.27	1					
NPU	-0.25	0.09	0.22	-0.25	-0.21	0.004	0.20	0.09	1				
LFD	**0.80**	0.49	-0.44	0.45	-0.09	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.25	-0.13	0.39	0.31	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.26	0.16	-0.25	0.22	-0.03	0.00007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.11	-0.14	0.08	-0.05	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Functional diversity													
	REG	FC (900m)	PC (400m)	ED (900m)	NFF (900m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (900m)	0.43	1											

PC (400m)	-0.49	-0.38	1										
ED (900m)	0.51	0.42	-0.41	1									
NFF (900m)	-0.06	-0.66	-0.05	0.12	1								
NCT	0.14	-0.04	-0.08	0.02	-0.18	1							
NST	0.29	0.46	-0.17	-0.07	-0.48	0.17	1						
NFT	0.06	0.08	-0.05	-0.13	-0.23	0.35	0.27	1					
NPU	-0.25	0.08	0.28	-0.18	-0.31	0.004	0.20	0.09	1				
LFD	**0.80**	0.46	-0.35	0.39	-0.30	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.27	-0.35	0.21	0.11	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.25	0.07	-0.34	-0.03	-0.03	0.00007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.09	-0.18	-0.1	0.15	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Phylogenetic richness													
	REG	FC (800m)	PC (1000m)	ED (1000m)	NFF (500m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (800m)	0.32	1											
PC (1000m)	-0.49	-0.42	1										
ED (1000m)	0.65	0.61	-0.45	1									
NFF (500m)	-0.06	-0.56	-0.05	-0.15	1								
NCT	0.14	-0.13	-0.08	-0.22	-0.18	1							
NST	0.29	0.40	-0.17	0.16	-0.48	0.17	1						
NFT	0.06	-0.01	-0.05	-0.12	-0.23	0.35	0.27	1					
NPU	-0.25	-0.03	0.28	-0.25	-0.31	0.004	0.20	0.09	1				
LFD	**0.80**	0.27	-0.35	0.45	-0.30	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.33	-0.35	0.39	0.11	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.16	0.07	-0.25	-0.03	-0.03	0.00007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.09	-0.11	0.12	-0.001	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Phylogenetic diversity													
	REG	FC (400m)	PC (400m)	ED (400m)	NFF (900m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (400m)	0.32	1											

PC (400m)	-0.49	-0.42	1										
ED (400m)	0.65	0.61	-0.45	1									
NFF (900m)	-0.06	-0.56	-0.05	-0.15	1								
NCT	0.14	-0.13	-0.08	-0.22	-0.18	1							
NST	0.29	0.40	-0.17	0.16	-0.48	0.17	1						
NFT	0.06	-0.01	-0.05	-0.12	-0.23	0.35	0.27	1					
NPU	-0.25	-0.03	0.28	-0.25	-0.31	0.003	0.20	0.09	1				
LFD	**0.80**	0.27	-0.35	0.45	-0.30	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.33	-0.35	0.39	0.11	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.16	0.07	-0.25	-0.03	-0.03	0.0007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.05	-0.18	0.08	0.15	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Reptiles													
Taxonomic richness													
	REG	FC (1000 m)	PC (500 m)	ED (500m)	NFF (900m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (1000m)	0.44	1											
PC (500m)	-0.48	-0.38	1										
ED (500m)	0.61	0.52	-0.42	1									
NFF (900m)	0.00	-0.46	0.19	0.08	1								
NCT	0.14	-0.02	-0.11	-0.17	-0.25	1							
NST	0.29	0.46	-0.19	0.13	-0.38	0.17	1						
NFT	0.06	0.10	-0.08	-0.10	-0.16	0.35	0.27	1					
NPU	-0.25	0.09	0.24	-0.22	-0.16	0.004	0.20	0.09	1				
LFD	**0.80**	0.49	-0.36	0.43	-0.12	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.25	-0.34	0.38	0.20	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.26	0.10	-0.21	-0.02	-0.03	0.0007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.11	-0.21	0.10	-0.002	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Taxonomic diversity													
	REG	FC (900m)	PC (500m)	ED (500m)	NFF (900m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												

FC (900m)	0.43	1											
PC (500m)	-0.48	-0.40	1										
ED (500m)	0.61	0.55	-0.42	1									
NFF (900m)	-0.06	-0.66	-0.02	-0.10	1								
NCT	0.14	-0.04	-0.11	-0.17	-0.18	1							
NST	0.29	0.46	-0.19	0.13	-0.48	0.17	1						
NFT	0.06	0.08	-0.08	-0.10	-0.23	0.35	0.27	1					
NPU	-0.25	0.08	0.24	-0.22	-0.31	0.004	0.20	0.09	1				
LFD	**0.80**	0.46	-0.36	0.43	-0.30	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.27	-0.34	0.38	0.11	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.25	0.10	-0.21	-0.03	-0.03	0.0007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.09	-0.21	0.10	0.15	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Functional richness													
	REG	FC (800m)	PC (500m)	ED (600m)	NFF (500m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (800m)	0.42	1											
PC (500m)	-0.48	-0.42	1										
ED (600m)	0.60	0.54	-0.44	1									
NFF (500m)	0.00	-0.49	0.19	0.15	1								
NCT	0.14	-0.05	-0.11	-0.12	-0.25	1							
NST	0.29	0.47	-0.19	0.05	-0.38	0.17	1						
NFT	0.06	0.07	-0.08	-0.11	-0.16	0.35	0.27	1					
NPU	-0.25	0.08	0.24	-0.23	-0.16	0.004	0.20	0.09	1				
LFD	**0.80**	0.44	-0.36	0.42	-0.12	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.28	-0.34	0.38	0.20	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.25	0.10	-0.30	-0.02	-0.03	0.0007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.09	-0.21	0.10	-0.002	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Functional diversity													
	REG	FC (800m)	PC (500m)	ED (700m)	NFF (500m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												

FC (800m)	0.44	1											
PC (500m)	-0.48	-0.38	1										
ED (700m)	0.60	0.51	-0.44	1									
NFF (500m)	0.00	-0.46	0.19	0.25	1								
NCT	0.14	-0.02	-0.11	-0.08	-0.13	1							
NST	0.29	0.46	-0.19	-0.01	-0.45	0.17	1						
NFT	0.06	0.10	-0.08	-0.16	-0.30	0.35	0.27	1					
NPU	-0.25	0.09	0.24	-0.25	-0.30	0.004	0.20	0.09	1				
LFD	**0.80**	0.49	-0.36	0.42	-0.28	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.25	-0.34	0.36	0.04	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.26	0.10	-0.34	-0.08	-0.03	0.0007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.11	-0.21	0.13	0.16	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Phylogenetic richness													
	REG	FC (1000m)	PC (500m)	ED (500m)	NFF (1000m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												
FC (1000m)	0.44	1											
PC (500m)	-0.48	-0.38	1										
ED (500m)	0.61	0.52	-0.42	1									
NFF (1000m)	-0.05	-0.66	0.02	-0.07	1								
NCT	0.14	-0.02	-0.11	-0.17	-0.13	1							
NST	0.29	0.46	-0.19	0.13	-0.45	0.17	1						
NFT	0.06	0.10	-0.08	-0.10	-0.30	0.35	0.27	1					
NPU	-0.25	0.09	0.24	-0.22	-0.30	0.004	0.20	0.09	1				
LFD	**0.80**	0.49	-0.36	0.43	-0.28	0.41	0.34	0.24	-0.07	1			
CC	0.21	0.25	-0.34	0.38	0.04	-0.30	0.19	0.17	-0.38	0.03	1		
AT	-0.46	-0.26	0.10	-0.21	-0.08	-0.03	0.0007	0.26	0.09	-0.37	0.15	1	
RH	0.36	0.11	-0.21	0.10	0.16	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60	1
Phylogenetic diversity													
	REG	FC (1000m)	PC (500m)	ED (500m)	NFF (900m)	NCT	NST	NFT	NPU	LFD	CC	AT	RH
REG	1												

FC (1000m)	0.44	1											
PC (500m)	-0.48	-0.38	1										
ED (500m)	0.61	0.52	-0.42	1									
NFF (900m)	-0.06	-0.67	-0.02	-0.10	0.69	1							
NCT	0.14	-0.02	-0.11	-0.17	-0.25	-0.18	1						
NST	0.29	0.46	-0.19	0.13	-0.38	-0.48	0.17	1					
NFT	0.06	0.10	-0.08	-0.10	-0.16	-0.23	0.35	0.27	1				
NPU	-0.25	0.09	0.24	-0.22	-0.16	-0.31	0.004	0.20	0.09	1			
LFD	**0.80**	0.49	-0.36	0.43	-0.12	-0.30	0.41	0.34	0.24	-0.07	1		
CC	0.21	0.25	-0.34	0.38	0.20	0.11	-0.30	0.19	0.17	-0.38	0.03	1	
AT	-0.46	-0.26	0.10	-0.21	-0.02	-0.03	-0.03	0.0007	0.26	0.09	-0.37	0.15	1
RH	0.36	0.11	-0.21	0.10	-0.002	0.15	0.10	0.29	-0.08	-0.35	0.19	0.03	-0.60

Appendix 5. Taxonomic, functional and phylogenetic metrics used to describe the communities of amphibian and reptile species.

Table S5. Observed (amphibians) and estimated (reptiles) values of taxonomic, functional and phylogenetic richness and diversity record in 30 shaded cocoa agroforest systems located in three different regions. ^{0}TD: taxonomic richness; ^{1}TD: taxonomic diversity; ^{0}FD: functional richness; ^{1}FD: functional diversity; ^{0}PD: phylogenetic richness; ^{1}PD: phylogenetic diversity. HAC: High Agroforest cover region; HFC: High Forest Cover region; LFC: Low Forest Cover region.

Region	**Site**	**Amphibians**						**Reptiles**					
		^{0}TD	**^{1}TD**	**^{0}FD**	**^{1}FD**	**^{0}PD**	**^{1}PD**	**^{0}TD**	**^{1}TD**	**^{0}FD**	**^{1}FD**	**^{0}PD**	**^{1}PD**
HAC	I10	22	13.82	2.76	2.49	1685.55	652.34	24.19	9.50	4.66	2.05	1357.98	831.21
HAC	I11	20	6.96	2.76	2.07	1655.68	545.99	6.53	3.42	2.06	1.53	613.75	421.98
HAC	I12	21	6.49	2.65	1.91	1663.98	541.69	9.88	5.69	2.43	1.73	866.12	622.59
HAC	I13	21	12.56	2.59	2.22	1494.09	598.96	7.48	5.75	2.17	1.78	838.72	653.78
HAC	I14	19	4.49	2.38	1.68	1501.02	480.69	22.28	8.56	3.14	1.84	1143.23	686.51
HAC	I15	24	6.59	2.76	2.14	1789.95	551.20	21.20	10.81	3.53	2.09	1384.12	890.69
HAC	I16	15	7.50	2.39	2.07	1189.52	535.62	17.57	5.49	3.06	1.59	865.33	552.87
HAC	I17	22	7.52	2.89	2.28	1597.79	564.14	15.66	8.81	3.27	1.92	1207.86	757.81
HAC	I4	18	7.24	2.62	2.05	1536.17	559.01	9.85	4.46	1.42	1.14	684.99	444.36
HAC	I8	18	5.17	2.47	1.77	1441.05	498.05	5.63	4.25	1.85	1.51	647.28	549.63
HFC	U1	14	6.40	2.19	1.97	1111.01	511.87	5.07	2.87	1.33	1.15	457.73	301.28
HFC	U11	21	9.41	2.71	2.29	1721.09	591.56	15.16	7.61	2.39	1.77	1203.87	707.88
HFC	U12	15	5.87	2.48	2.17	1291.49	530.61	10.49	7.62	4.11	2.74	852.86	676.62
HFC	U13	26	6.17	2.47	1.85	1789.51	502.77	3.62	2.80	1.34	1.33	354.56	330.13
HFC	U14	9	2.21	2.22	1.38	951.63	382.46	5.91	4.95	2.46	2.06	739.14	602.66
HFC	U15	20	7.92	2.57	1.95	1563.37	541.83	19.56	8.69	4.38	2.00	1376.96	677.28
HFC	U16	14	3.83	2.10	1.70	1151.68	477.48	7.03	4.83	2.60	2.01	807.58	636.90

HFC	U17	16	5.37	2.53	1.86	1366.70	498.46	19.84	10.85	5.59	2.96	1598.69	849.53
HFC	U3	15	6.04	2.38	2.01	1277.55	522.23	19.61	7.30	3.31	1.88	1119.13	652.21
HFC	U7	22	8.37	2.51	2.11	1738.51	579.11	10.60	6.70	2.53	1.79	1034.90	660.43
LFC	B13	21	10.16	2.68	1.99	1733.54	601.07	12.01	7.76	3.53	2.73	833.86	626.86
LFC	B14	22	8.35	2.51	2.08	1429.75	529.92	17.70	8.86	2.69	1.81	1127.54	688.91
LFC	B15	16	6.46	2.27	2.02	1312.31	565.96	6.20	3.19	2.45	1.67	479.81	397.82
LFC	B16	22	10.51	2.86	2.38	1746.41	614.13	13.55	9.71	3.19	2.58	786.15	607.73
LFC	B18	16	6.18	2.60	1.99	1327.69	528.47	5.12	3.65	1.69	1.44	433.03	379.12
LFC	B19	21	5.21	2.65	1.64	1694.61	470.26	5.08	3.34	1.93	1.62	501.14	424.55
LFC	B20	19	8.81	2.62	2.20	1571.61	568.98	6.43	3.95	1.76	1.46	512.23	422.25
LFC	B21	25	12.07	2.83	2.28	1839.86	594.86	7.34	3.30	2.31	1.56	433.53	364.23
LFC	B7	32	15.00	3.10	2.24	2348.88	656.21	13.45	9.10	3.74	2.87	1191.80	785.49
LFC	B9	23	13.85	2.53	2.15	1608.39	617.54	17.30	9.32	3.62	1.85	910.47	579.13

Appendix 6. List of amphibian and reptile species recorded in 30 shaded agroforest systems located in three different regions in the southern Bahia state, Brazil. For each species, we also indicated the number of individuals recorded and ecological traits used to estimate functional metrics

Table S6. List of amphibian (Anura and Gymnophiona) and reptile (Squamata-Ophidia and Squamata-Lacertilia) species and families recorded in 30 shaded agroforest systems of the three regions (HAC, HFC and LFC) of Bahia state, Brazil. For each species, the total abundances recorded per region are presented, as well as their respective ecological traits classified from the databases obtained in specific literatures (see Appendix 2). HAC: High Agroforest cover region; HFC: High Forest Cover region; LFC: Low Forest Cover region. Activity time: diurnal (1); nocturnal (2); diurnal-nocturnal (3). Microhabitat: Fossorial (1); terrestrial (2); aquatic (3); arboreal (4); semi-arboreal (5) and semi-aquatic (6). Reproductive mode for amphibians: eggs in water and larval development in water (1); eggs in vegetation and larval development in water (2); terrestrial eggs with indirect development in foam (3); terrestrial eggs with direct development (4). Reproductive mode for reptiles: oviparous (1) and viviparous (2).

ORDER (Suborder)		**Regions**			**Ecological traits**				
Family	**Species**	**HAC**	**HFC**	**LFC**	**Body length mm**	**Biomass (g)**	**Activity**	**Microhabitat**	**Reproductive mode**
ANURA	ANURA								
Allophrynidae	*Allophryne relicta*	0	0	4	21.9	-	2	4	1
Aromobatidae	*Allobates olfersioides*	317	154	150	19	-	1	3	2
Bufonidae	*Rhinella crucifer*	32	84	23	68.2	-	2	2	1
Bufonidae	*Rhinella granulosa*	1	0	1	64.47	-	2	2	1
Bufonidae	*Rhinella hoogmoedi*	768	376	211	63.94	-	2	2	1
Centrolenidae	*Vitreorana baliomma*	0	1	2	21.2	-	2	4	1

Craugastoridae	*Haddadus binotatus*	102	30	291	60.94	-	2	2	4
Cycloramphidae	*Thoropa miliaris*	0	1	6	83.66	-	2	2	2
Eleutherodactylidae	*Adelophryne mucronatus*	2	12	0	14.9	-	2	2	4
Hemiphractidae	*Gastrotheca recava*	0	1	9	84.9	-	2	4	4
Hylidae	*Aplastodiscus ibirapitanga*	0	4	0	45	-	2	4	1
Hylidae	*Boana albomarginata*	10	4	6	53	-	2	2	1
Hylidae	*Boana atlantica*	21	0	10	43.5	-	2	2	1
Hylidae	*Boana crepitans*	8	9	11	60.33	-	2	2	1
Hylidae	*Boana exastis*	0	4	2	99	-	2	2	1
Hylidae	*Boana faber*	13	6	28	98.9	-	2	2	1
Hylidae	*Boana pombali*	16	1	2	65.7	-	2	2	1
Hylidae	*Boana semilineata*	30	19	39	48.5	-	2	2	1
Hylidae	*Bokermannohyla capra*	0	1	2	64.1	-	2	4	1
Hylidae	*Dendropsophus anceps*	0	1	0	42	-	2	4	1
Hylidae	*Dendropsophus branneri*	2	3	9	23.6	-	2	4	1
Hylidae	*Dendropsophus elegans*	5	5	34	22	-	2	4	2
Hylidae	*Dendropsophus haddadi*	8	2	1	27	-	2	4	1
Hylidae	*Dendropsophus minutus*	0	0	5	27.64	-	2	4	1
Hylidae	*Dendropsophus novaisi*	0	0	1	36	-	2	4	1
Hylidae	*Dendropsophus seniculus*	1	0	1	43	-	2	4	1
Hylidae	*Hylomantis granulosa*	0	0	1	38.7	-	2	4	2
Hylidae	*Itapotihyla langsdorffii*	15	7	11	97.52	-	2	4	1
Hylidae	*Nyctimantis brunoi*	0	22	8	81	-	2	4	1

Hylidae	*Ololygon argyreornata*	1	5	42	23	-	2	4	1
Hylidae	*Ololygon strigilata*	19	77	286	38.3	-	2	4	1
Hylidae	*Phyllodytes wuchereri*	2	6	0	26	-	2	4	1
Hylidae	*Phyllodytes luteolus*	13	1	0	41.1	-	2	4	1
Hylidae	*Phyllodytes magnus*	0	5	0	49	-	2	4	1
Hylidae	*Phyllodytes melanomystax*	1	1	0	27.1	-	2	4	2
Hylidae	*Phyllomedusa bahiana*	0	4	10	85	-	2	4	2
Hylidae	*Phyllomedusa burmeisteri*	1	4	2	76.7	-	2	4	2
Hylidae	*Pithecopus nordestinus*	3	0	3	48.3	-	2	4	2
Hylidae	*Pithecopus rohdei*	11	0	7	38.9	-	2	4	4
Hylidae	*Scinax cuspidatus*	0	1	3	32.5	-	2	4	1
Hylidae	*Scinax eurydice*	2	14	27	53.95	-	2	4	1
Hylidae	*Scinax fuscomarginatus*	0	0	3	21.89	-	2	4	1
Hylidae	*Scinax fuscovarius*	2	0	15	47.6	-	2	4	1
Hylidae	*Scinax juncae*	4	1	0	27	-	2	4	1
Hylidae	*Scinax nebulosus*	0	0	2	23.8	-	2	6	1
Hylidae	*Scinax similis*	0	1	1	36.4	-	2	4	1
Hylidae	*Scinax x-signatus*	3	1	17	25.1	-	2	4	1
Hylidae	*Sphaenorhynchus pauloalvini*	0	0	4	31	-	2	4	2
Hylidae	*Trachycephalus mesophaeus*	26	16	17	73.11	-	2	4	1
Hylidae	*Trachycephalus nigromaculatus*	0	0	2	91.1	-	2	4	1
Leptodactylidae	*Adenomera thomei*	48	7	67	23.2	-	2	2	3
Leptodactylidae	*Leptodactylus fuscus*	6	0	20	56.7	-	2	2	2

Leptodactylidae	*Leptodactylus latrans*	54	51	58	65.38	-	2	2	2
Leptodactylidae	*Leptodactylus mystaceus*	38	35	143	43.07	-	2	2	2
Leptodactylidae	*Leptodactylus mystacinus*	1	0	0	69.9	-	2	2	2
Leptodactylidae	*Leptodactylus natalensis*	45	14	13	55	-	2	2	2
Leptodactylidae	*Leptodactylus troglodytes*	4	0	2	48	-	2	2	2
Leptodactylidae	*Physalaemus camacan*	265	309	192	23.3	-	2	2	2
Leptodactylidae	*Physalaemus cicada*	2	0	0	25.4	-	2	5	2
Leptodactylidae	*Physalaemus erikae*	33	55	142	27.1	-	2	2	1
Microhylidae	*Chiasmocleis cordeiroi*	3	5	11	22.1	-	2	5	1
Microhylidae	*Chiasmocleis crucis*	0	4	3	20.2	-	2	2	1
Microhylidae	*Chiasmocleis schubarti*	6	4	41	34.5	-	2	2	1
Microhylidae	*Stereocyclops incrassatus*	1	2	1	57.8	-	2	2	1
Odontophrynidae	*Macrogenioglottus alipioi*	4	0	1	108.8	-	2	2	1
Odontophrynidae	*Odontophrynus carvalhoi*	0	0	1	74.58	-	2	2	1
Odontophrynidae	*Proceratophrys renalis*	13	2	6	71.9	-	2	2	1
Odontophrynidae	*Proceratophrys schirchi*	0	0	1	46	-	2	2	1
Pipidae	*Pipa carvalhoi*	0	0	2	68.4	-	3	3	1
Strabomantidae	*Bahius bilineatus*	17	0	0	26	-	2	2	1
Strabomantidae	*Pristimantis paulodutrai*	698	814	293	36	-	2	2	4
Strabomantidae	*Pristimantis* sp.	9	0	0	36	-	2	2	4
Strabomantidae	*Pristimantis vinhai*	25	49	30	25	-	2	2	1
GYMNOPHIONA	GYMNOPHIONA					-			
Siphonopidae	*Siphonops annulatus*	0	0	1	454	-	2	1	4

SQUAMATA (Ophidia)									
Boidae	*Corallus hortulanus*	0	0	2	1887	3922.3	2	4	2
Boidae	*Epicrates cenchria*	0	1	0	2200	4570.5	2	2	2
Colubridae	*Chironius bicarinatus*	0	1	0	1800	521.4	1	5	1
Colubridae	*Chironius exoletus*	1	1	1	1545	353.7	1	5	1
Colubridae	*Chironius fuscus*	1	0	0	1597	384.8	1	5	1
Colubridae	*Drymarchon corais*	2	0	0	2630	1365.4	1	5	1
Colubridae	*Leptophis ahaetulla*	1	0	0	2250	918.7	1	5	1
Colubridae	*Oxybelis aeneus*	1	0	0	1524	341.7	1	5	1
Dipsadidae	*Atractus guentheri*	0	0	1	479	26.1	3	1	1
Dipsadidae	*Dipsas albifrons*	0	1	4	590	75.4	2	5	1
Dipsadidae	*Dipsas catesbyi*	0	0	1	705	69.5	2	5	1
Dipsadidae	*Dipsas indica*	1	1	4	1028	180.9	3	5	1
Dipsadidae	*Dipsas neuwiedi*	1	2	0	660	100.4	2	5	1
Dipsadidae	*Dipsas variegata*	1	0	3	912	133.5	2	4	1
Dipsadidae	*Erythrolamprus aesculapii*	1	0	0	927	139.2	1	2	1
Dipsadidae	*Erythrolamprus miliaris*	0	0	1	684	110	3	6	1
Dipsadidae	*Erythrolamprus reginae*	2	0	0	810	98.8	1	1	1
Dipsadidae	*Imantodes cenchoa*	1	5	0	1554	515.8	2	4	1
Dipsadidae	*Oxyrhopus guibei*	5	1	1	1080	354.5	3	2	1
Dipsadidae	*Oxyrhopus petolarius*	0	2	1	2200	1245.6	3	2	1
Dipsadidae	*Siphlophis compressus*	1	0	2	1431	418.5	2	5	1
Dipsadidae	*Xenopholis scalaris*	3	3	0	354	12.1	3	2	1

Elapidae	*Micrurus corallinus*	0	0	1	987	244.5	1	1	1
Leptotyphlopidae	*Trilepida salgueiroi*	1	0	0	329	6.7	3	4	1
Viperidae	*Bothrops jararaca*	0	1	5	1600	2046.4	2	2	2
Viperidae	*Bothrops leucurus*	0	1	0	1950	3639.2	2	2	2
SQUAMATA (Sauria)									
Anguidae	*Diploglossus fasciatus*	0	1	0	170	99.3	1	2	1
Anolidae	*Anolis fuscoauratus*	74	49	130	52	3	1	5	1
Anolidae	*Anolis punctatus*	12	5	36	92	16	1	4	1
Gekkonidae	*Gymnodactylus darwinii*	22	7	14	59.1	5.1	2	5	1
Gymnophthalmidae	*Leposoma scincoides*	104	46	194	45.9	2	1	2	1
Leiosauridae	*Enyalius catenatus*	11	11	8	110	41.9	1	5	1
Phyllodactylidae	*Phyllopezus lutzae*	9	3	7	68.8	8.5	2	4	1
Polychrotidae	*Polychrus marmoratus*	3	0	6	148	101.2	1	5	1
Scincidae	*Psychosaura macrorhyncha*	11	0	14	85	12.7	1	4	2
Sphaerodactylidae	*Coleodactylus meridionalis*	62	1	0	30.5	0.6	1	2	1
Teiidae	*Ameiva ameiva*	1	1	2	210	298.6	1	2	1
Teiidae	*Kentropyx calcarata*	30	9	5	119	51	1	5	1
Teiidae	*Salvator merianae*	5	3	5	501	4434	1	2	1
Tropiduridae	*Tropidurus torquatus*	24	4	17	134	79.2	1	5	1

Appendix 7. Model selection parameters based on Akaike's Information Criterion (AICc), used to explain the relationship between environmental predictors and multiple dimensions of amphibian and reptile diversity. We also indicated the results of the DHARMa test for each parsimonious model.

Table S7. Results of model selection and DHARMa tests for the parsimonious models used to explain the effect of the environmental predictors on taxonomic, functional and phylogenetic richness and diversity of amphibian and reptile communities. For each model, we indicated AICc value, number of parameters of the model (k), AICc weight (wi), heteroscedasticity (KS-test) and overdispersion (Dispersion test).

Amphibians					
Species richness					
Models	AICc	K	wi	KS test p	Dispersion test p
Pasture cover	169.83	2	0.40	0.82	0.29
Pasture cover + Number of fallen trunks	171.73	3	1.90	0.74	0.26
Pasture cover + Number of shade trees	171.79	3	1.95	0.83	0.28
Pasture cover + Forest edge density	171.79	3	1.96	0.83	0.28
Pasture cover + Air temperature	171.82	3	0.1.99	0.89	0.28
Species diversity					
Models	AICc	k	wi	KS test p	Dispersion test p
Pasture cover + Number of understory vegetation	145.5	4	0.103	0.57	0.99
Pasture cover + Number of forest fragments	146.2	4	0.075	0.98	0.8
Pasture cover	146.3	3	0.07	0.86	0.83
Pasture cover + Number of forest fragments + Number of understory vegetation	147.1	5	0.047	0.5	0.86
Pasture cover + Number of forest fragments + Relative humidity	147.2	5	0.046	0.85	0.91
Functional richness					

Models	AICc	k	Wi	KS test p	Dispersion test p
Region	-5.6	4	0.066	0.99	0.86
Region + Relative humidity	-5.4	5	0.062	0.84	0.91
Canopy cover + Region	-4.4	5	0.037	0.73	0.88
Number of fallen trunks + Region	-3.9	5	0.029	0.67	0.82
Pasture cover + Region	-3.9	5	0.028	0.78	0.87
Forest edge density	-3.9	3	0.028	0.79	0.86
Air temperature + Region	-3.8	5	0.027	0.81	0.85
Forest edge density + Canopy cover	-3.8	4	0.027	0.99	0.9
Functional diversity					
Models	AICc	k	Wi	KS test p	Dispersion test p
Pasture cover + Number of forest fragments	0.87	4	0.078	0.49	0.96
Number of forest fragments	1.26	3	0.064	0.69	0.96
Native forest cover + Number of forest fragments	1.34	4	0.061	0.46	0.95
Number of forest fragments + Number of shade trees	1.92	4	0.046	0.74	1
Pasture cover + Number of forest fragments + Number of shade trees	2.38	5	0.036	0.29	1
Native forest cover + Number of forest fragments + Number of shade trees	2.53	5	0.034	0.59	0.97
Pasture cover + Number of forest fragments + Number of fallen trunks	2.63	5	0.032	0.3	0.96
Number of forest fragments + Canopy cover	2.68	4	0.031	0.35	0.98
Phylogenetic richness					
Models	AICc	k	Wi	KS test p	Dispersion test p
Pasture cover	421.8	3	0.062	0.37	0.89
Native forest cover	422.5	3	0.042	0.84	0.85
Pasture cover + Forest edge density	422.9	4	0.036	0.8	0.92
Forest edge density	423.1	3	0.033	0.51	0.82
Native forest cover + Forest edge density	423.3	4	0.029	0.97	0.82
Pasture cover + Number of fallen trunks	423.7	4	0.024	0.44	0.97

Phylogenetic diversity					
Models	AICc	k	Wi	KS test p	Dispersion test p
Native forest cover	331.4	3	0.0394	0.93	0.92
Region	332.0	4	0.0295	0.54	0.96
Pasture cover + Number of forest fragments	332.0	4	0.0295	0.57	0.93
Number of forest fragments + Region	332.1	5	0.0285	0.59	1
Native forest cover + Number of forest fragments	332.2	4	0.0267	0.64	0.92
Forest edge density	332.2	3	0.0266	0.51	0.9
Pasture cover + Number of understory plants	332.5	4	0.0225	0.77	0.94
Pasture cover + Number of fallen trunks	332.5	4	0.0225	0.85	0.94
Pasture cover + Forest edge density	332.9	4	0.0188	0.71	0.94
Number of forest fragments + Region + Relative humidity	333.0	6	0.0177	0.45	0.98
Null model	333.1	2	0.0166	0.98	0.88
Pasture cover + Canopy cover	333.4	4	0.0149	0.85	0.94
Reptiles					
Species richness					
Models	AICc	k	Wi	KS test p	Dispersion test p
Native forest cover	165.2	3	0.075	0.62	0.95
Forest edge density	165.4	3	0.066	0.78	0.84
Native forest cover + Forest edge density	165.9	4	0.053	0.87	0.96
Native forest cover + Relative humidity	166.2	4	0.046	0.65	1
Forest edge density + Relative humidity	166.9	4	0.031	0.71	0.87
Native forest cover + Number of fallen trunks	167.0	4	0.031	0.65	0.96
Forest edge density + Number of shade trees	167.1	4	0.028	0.42	0.71
Species diversity					
Models	AICc	k	Wi	KS test p	Dispersion test p
Native forest cover	130.8	3	0.070	0.85	0.9
Forest edge density	130.9	3	0.067	0.85	0.84
Native forest cover + Relative humidity	131.6	4	0.047	0.81	0.96
Native forest cover + Forest edge density	132.0	4	0.038	0.95	0.92

Forest edge density + Relative humidity	132.3	4	0.034	0.94	1
Functional richness					
Models	AICc	k	Wi	KS test p	Dispersion test p
Forest edge density + Relative humidity	70.0	4	0.115	0.71	0.66
Relative humidity	70.5	3	0.090	0.99	0.64
Native forest cover + Relative humidity	70.6	4	0.085	0.99	0.62
Native forest cover + Number of forest fragments + Relative humidity	71.0	5	0.068	0.86	0.61
Air temperature	71.8	3	0.046	0.85	0.55
Functional diversity					
Models	AICc	k	Wi	KS test p	Dispersion test p
Relative humidity	29.1	3	0.183	0.45	0.70
Forest edge density + Relative humidity	29.5	4	0.152	0.52	0.77
Number of forest fragments + Relative humidity + Region	30.7	6	0.081	0.71	0.94
Number of forest fragments + Relative humidity	30.7	4	0.080	0.3	0.72
Phylogenetic richness					
Models	AICc	k	Wi	KS test p	Dispersion test p
Forest edge density	433.4	3	0.067	0.99	0.73
Native forest cover	433.4	3	0.065	0.97	0.92
Native forest cover + Relative humidity	433.9	4	0.052	0.85	0.91
Forest edge density + Relative humidity	434.2	4	0.044	0.87	0.91
Native cover + Forest edge density	434.2	4	0.044	0.99	0.81
Forest edge density + Number of shade trees	434.6	4	0.035	0.93	0.66
Native forest cover + Forest edge density + Relative humidity	435.1	5	0.028	0.95	8.88
Phylogenetic diversity					
Models	AICc	k	Wi	KS test p	Dispersion test p
Native forest cover + Relative humidity	392.1	4	0.07197112	0.93	0.88
Native forest cover	392.1	3	0.0719132	0.88	0.98
Forest edge density	393.4	3	0.0380139	0.59	0.9

Forest edge density + Relative humidity	393.7	4	0.03289068	0.57	0.99
Native forest cover + Number of understory plants	393.9	4	0.03001117	0.92	0.97
Relative humidity	393.9	3	0.02882349	0.66	0.92
Native forest cover + Forest edge density	394.0	4	0.02789791	0.72	0.95

Appendix 8. Spatial autocorrelation test.

Table S8. Spatial autocorrelation test of conditional average models used to explain the relationship between landscape and local predictors and taxonomic, functional and phylogenetic metrics.

Amphibian species richness		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Pasture cover Forest edge density Number of shade trees Number of fallen trunks Air temperature	0.34	0.37
Amphibian species diversity		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Pasture cover Number of forest fragments Number of understory plants Relative humidity	0.01	0.49
Amphibian functional Richness		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Pasture cover Forest edge density Number of fallen trunks Canopy cover Air temperature Relative humidity Region: High Agroforest Cover Region: High Forest Cover	0.76	0.22
Amphibian functional diversity		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Native forest cover Pasture cover Number of forest fragments Number of shade trees	1.65	0.053

Number of fallen trunks Canopy cover		
Amphibian phylogenetic richness		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Native forest cover Pasture cover Forest edge density Number of fallen trunks	0.70	0.24
Reptile species richness		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Native forest cover Forest edge density Number of shade trees Number of fallen trunks Relative humidity	0.54	0.29
Reptile species diversity		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Native forest cover Forest edge density Relative humidity	0.56	0.29
Reptile functional Richness		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Native forest cover Forest edge density Number of forest fragments Air temperature Relative humidity	0.06	0.48
Reptile functional diversity		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Forest edge density Number of forest fragments Relative humidity Region: High Agroforest Cover Region: High Forest Cover	-0.25	0.60

Reptile phylogenetic richness		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Native forest cover Forest edge density Number of shade trees Relative humidity	-0.74	0.77
Reptile phylogenetic diversity		
Model conditional average	I Moran statistic standard deviate	P-value
Intercept Native forest cover Forest edge density Number of understory plants Relative humidity	-0.17	0.56

Appendix 9. Test of phylogenetic signal for ecological traits used in our study.

Table S9. Phylogenetic signal analysis for ecological traits in amphibian and reptile communities. We indicated D value for categorical traits and Blomberg's K for continuous traits. The D-value measures the presence of phylogenetic signals in categorical ecological traits. A D-value of 1 indicates that a trait is randomly distributed across the phylogenetic tree, while values below 0 reflect a strongly clustered distribution. For continuous traits, Blomberg's K is used; significant values of K < 1 or K > 1 indicate weaker or stronger phylogenetic signals, respectively, compared to what would be expected under a Brownian motion model.

Group	**Ecological trait**	**Atributes**	**Phylogenetic signal (D value or Blomberg`s K)**	**P-value**
Amphibians	Body length	-	1.31	0.778
	Activity time	Diurnal	-2.36	**0.011**
		Nocturnal	-1.65	**0.004**
		Both	-2.28	**0.019**
	Microhabitat	Fossorial	-3.38	**<0.01**
		Terrestrial	-1.17	**<0.01**
		Aquatic	-1.64	**0.008**
		Arboreal	-1.40	**<0.01**
		Semi-arboreal	1.39	0.665
		Semi-aquatic	1.07	0.417
	Reproductive mode	Eggs in water and larval development in water	-0.60	**<0.01**
		Eggs in vegetation and larval development in water	-0.52	**<0.01**
		Terrestrial eggs with indirect development in foam	0.05	0.226
		Terrestrial eggs with direct development	-0.42	**0.002**
Reptiles	Body length	-	2.77	0.978
	Body mass	-	0.92	0.607
	Activity time	Diurnal	-0.69	**<0.01**
		Nocturnal	-0.15	**0.002**
		Both	0.38	0.053

	Microhabitat	Fossorial	0.99	0.423
		Terrestrial	0.17	**0.007**
		Arboreal	0.89	0.335
		Semi-arboreal	0.24	**0.008**
		Semi-aquatic	2.47	0.615
	Reproductive mode	Oviparous	-1.00	**<0.01**
		Viviparous	-1.14	**<0.01**

Chapter 3. Patterns and predictors of taxonomic, functional and phylogenetic beta diversity of amphibian and reptile communities in shaded cocoa agroforest

O presente capítulo será submetido para a revista Biodiversity and Conservation. Portanto, a formatação segue as normas da revista.

Patterns and predictors of taxonomic, functional and phylogenetic beta diversity of amphibian and reptile communities in shaded cocoa agroforest

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Abstract

The loss and fragmentation of natural landscapes reshape amphibian and reptile communities, altering beta diversity patterns in response to environmental heterogeneity and geographic distance—even in modified habitats such as shaded cocoa agroforests. In this study, we evaluated taxonomic, functional, and phylogenetic beta diversity of amphibians and reptiles across 30 cocoa agroforests distributed in three regions with contrasting land-use contexts: high agroforest cover (HAC), high forest cover (HFC), and low forest cover (LFC). We examined how landscape (forest and pasture cover), local (number of shaded trees and canopy cover), and spatial (geographic distance) predictors influence beta diversity. Overall, beta diversity was low across all dimensions. Amphibians showed higher values in LFC, while reptiles peaked in HFC; both groups had the lowest values in HAC. In HAC, amphibian beta diversity declined with variation in shade tree abundance and canopy cover, whereas in HFC it increased with variation in shade trees and pasture cover. Amphibian beta diversity in LFC increased with geographic distance. For reptiles, beta diversity in HAC was associated with canopy cover, while in HFC it was influenced by forest cover and spatial distance. In LFC, only phylogenetic beta diversity responded, decreasing with variation in grass cover and increasing with distance. These contrasting patterns underscore the need to assess multiple biodiversity dimensions across landscape contexts to understand the mechanisms driving community structure in agroforests.

***Key words*:** Agroforest System, Atlantic Forest, Herpetofauna, Environmental heterogeneity, Landscape fragmentation, Species composition.

Introduction

As human populations expand, the growing demand for space, food, and energy continues to drive the loss, fragmentation, and degradation of native forests (Curtis et al. 2018). These anthropogenic changes profoundly affect biodiversity by reducing habitat heterogeneity, altering environmental conditions, limiting dispersal, and increasing genetic isolation among populations (Fahrig 2003, 2017). Consequently, species communities are reshaped along environmental and spatial gradients in human-modified landscapes.

A key metric for quantifying these compositional changes is beta diversity, which measures variation in species composition across spatial and environmental gradients (Whittaker 1972; Tuomisto 2010). By assessing how communities differ among sites, beta diversity provides essential information on the processes driving changes in species composition and biodiversity patterns in both natural and modified habitats (Socolar et al. 2016; Blowes et al. 2024). For example, low beta diversity indicates greater compositional similarity among communities, whereas high beta diversity reflects stronger differentiation (Anderson et al. 2011; Maurenza et al. 2024). Although high beta diversity is not always a desirable conservation outcome, as it may be the result of perturbations or stochastic processes, (such as dispersal limitation or ecological drift) in degraded habitats, it is still crucial to understand its underlying drivers (Socolar et al. 2016). Therefore, beta diversity plays a key role in conservation planning, such as identifying priority areas, predicting species loss, and designing wildlife-friendly landscapes or reserve networks that adequately represent regional biodiversity (Ochoa-Ochoa et al. 2014; Socolar et al. 2016).

Beyond its relevance for conservation planning, beta diversity is shaped by ecological and spatial processes operating across multiple scales (Arroyo-Rodríguez et al. 2013; Morante-Filho et al. 2016; Arce-Peña et al. 2022). Habitat loss and increased isolation can limit species dispersal, leading to greater differentiation in species composition across sites (Da Silva et al. 2014; Morante-Filho et al. 2016; Wayman et al. 2024). At the same time, environmental heterogeneity at both local and landscape levels creates distinct microhabitats, resource availability, and species interactions, influencing community composition through environmental filtering (Da Cunha Bitar et al. 2015; Morante-Filho et al. 2016; Neilan et al. 2019; Medeiros et al. 2019). These mechanisms have been empirically documented across various taxa. For example, in the Brazilian

Atlantic Forest, bird beta diversity is shaped by geographic isolation and differences in forest and pasture cover, with lower beta values found in less forested regions (Morante-Filho et al. 2016). Similarly, in highly deforested regions with limited connectivity, tropical plant communities show increased beta diversity driven by reduced seed dispersal and divergent successional trajectories (Arroyo-Rodríguez et al. 2013). These findings underscore the importance of considering not only local environmental variation but also the broader landscape context—including landscape composition—when assessing biodiversity patterns. Therefore, evaluating how beta diversity varies among regions with contrasting land-use histories can provide key insights into the role of landscape structure in shaping species composition.

In addition to taxonomic variation, incorporating functional and phylogenetic dimensions of beta diversity has become increasingly important for understanding how communities are structured and how biodiversity responds to environmental change (Devictor et al. 2010; Wang et al. 2022; Li et al. 2024). Functional beta diversity reflects differences in species' ecological roles based on their traits (Ricotta and Pavoine 2024), while phylogenetic beta diversity captures variation in evolutionary relationships among species (Graham and Fine 2008). Relying solely on taxonomic metrics may overlook important functional and evolutionary differences, as these indices treat all species as ecologically and phylogenetically equivalent (Arnan et al. 2015). Moreover, taxonomic, functional, and phylogenetic beta diversity may respond differently to environmental and spatial gradients, revealing distinct assembly processes (Leão-Pires et al. 2018; De Fraga et al. 2018; Li et al. 2024). For instance, Li et al. (2024), studying macroinvertebrates in the Wei River Basin, found that while local environmental variables shaped taxonomic and phylogenetic beta diversity, spatial factors exerted a stronger influence on functional beta diversity. Similarly, in the Atlantic Forest, tadpole communities showed that canopy cover and vegetation structure shaped taxonomic and functional beta diversity, whereas phylogenetic beta diversity reflected broader-scale spatial structuring, likely linked to biogeographic patterns (Leão-Pires et al. 2018). These findings reinforce the importance of adopting a multidimensional approach to better understand the mechanisms underlying community differentiation and to inform more integrative conservation strategies.

Shaded agroforests, such as cocoa systems, provide a valuable context to investigate patterns of beta diversity and the mechanisms driving community differentiation across local and landscape scales. In these agroecological matrix, cocoa trees are cultivated beneath a canopy of native and commercial shade trees, which can maintain habitat complexity and resource availability, thereby supporting diverse biological communities (Rice and Greenberg 2000; Schroth et al. 2011; Merijn and Sporn 2012). However, both local management intensity (Deheuvels et al. 2014; Bohada-Murillo et al. 2020) and the surrounding landscape context (Faria et al. 2007; Medeiros et al. 2019; Cervantes-López et al. 2025) can alter environmental heterogeneity and, consequently, species composition. Amphibians and reptiles are particularly suitable taxa for investigating these dynamics due to their sensitivity to microclimatic and habitat changes, limited dispersal abilities, and key ecological functions (Cortéz-Gómez et al. 2015; Cox et al. 2022; Luedtke et al. 2023). Their community structure and diversity are strongly influenced by both habitat characteristics and broader landscape features (Cervantes-López et al. 2025; Mesquita et al. 2025), making them excellent indicators for understanding how environmental heterogeneity and spatial configuration shape biodiversity in human-modified landscapes.

In this study we assessed the patterns and predictors of taxonomic, functional, and phylogenetic beta diversity of amphibian and reptile communities across 30 shaded cocoa agroforestry systems distributed among three regions with contrasting land-use contexts in the Brazilian Atlantic Forest. Firstly, we analyzed whether beta diversity patterns across all dimensions differed among the three regions. Secondly, we explored how variation in landscape (native forest and pasture cover), local (vegetation structure), and spatial (geographic distance) predictors shaped the beta diversity of each taxon and diversity dimension within each region.

We expect that the most degraded region—characterized by low forest cover and high pasture dominance—will exhibit lower beta diversity across all dimensions for both groups, due to strong environmental filtering that selects species tolerant to harsh conditions and limits habitat availability (Da Cunha Bitar et al. 2015; Morante-Filho et al. 2016). Conversely, we hypothesized that geographic distance and environmental dissimilarity—based on both landscape and local predictors—would differentially influence taxonomic, functional, and phylogenetic beta diversity. Specifically, we expected taxonomic and phylogenetic beta diversity to increase with greater differences among sites, reflecting species dispersal limitations and environmental filtering processes (Arroyo-Rodríguez et al. 2013; Morante-Filho et al. 2016; Palmeirim et al. 2017; Nowakowski et al. 2018a). In contrast, we predicted that functional beta diversity would show weaker responses to these predictors, as many amphibians and reptiles in the region share similar ecological traits despite differences in taxonomy or phylogeny. This expectation is supported by previous findings in the same system, where taxonomic and phylogenetic alpha diversity exhibited closely related patterns, suggesting that functional redundancy among species may dampen trait-based turnover (Cervantes-López et al., 2025).

Methods

Study area

The study was conducted in the southeastern of Bahia, Brazil, an area characterized by a mosaic of native forest patches surrounded by anthropogenic matrices (Figure 1) (Bandeira and Morante-Filho 2024). The remaining native forests in this area belong to the Atlantic Forest, one of the world's most biodiverse biomes, presenting high endemism of several taxonomic groups, including amphibians and reptiles (Figueiredo et al. 2021). On the other hand, the agricultural matrices consist of cattle pastures, eucalyptus plantations, and shaded cocoa agroforest system. The latter system consists of cocoa trees planted beneath the canopy of native Atlantic Forest tree species, alongside commercially valuable trees such as cashew (*Anacardium occidentale*), jackfruit (*Artocarpus heterophyllus*) or cajá tree (*Spondias mombin*) (Figueiredo 2024).

Based on the Köppen climate classification, the study area experiences a predominantly warm and wet climate for the majority of the year (Aw), without a distinct dry season. However, a relatively drier period occurs between December and March (Thomas et al. 1998). The average yearly temperature is 24°C, and the annual rainfall ranges between 1,500 and 2,000 mm.

We selected 30 shaded cocoa agroforests, with a minimum distance of 2 km among them, ranging from 4 to over 100 hectares, and distributed across three regions with varying forest cover and land use history (Figure 1). The northernmost region, referred to as High Agroforest Cover (HAC) region, is highly heterogeneous, characterized by a substantial presence of shaded cocoa agroforests (39%), moderate forest cover (42%), and limited of pasture areas (8%). The central region, referred to as High Forest Cover (HFC) region is defined by extensive forest cover (53%), largely preserved by three protected areas: Una Biological Reserve, Una Wildlife Refuge, and Serra das Lontras National Park. This region contains a moderate proportion of shaded cocoa agroforests (23%) and low pasture cover (12%). The southernmost region, referred to as Low Forest Cover (LFC) region, experiences the highest deforestation rates; it is dominated by cattle pastures (30%), reduced forest cover (32%), a lower proportion of shaded cocoa agroforests (17%), and some eucalyptus plantations (6%).

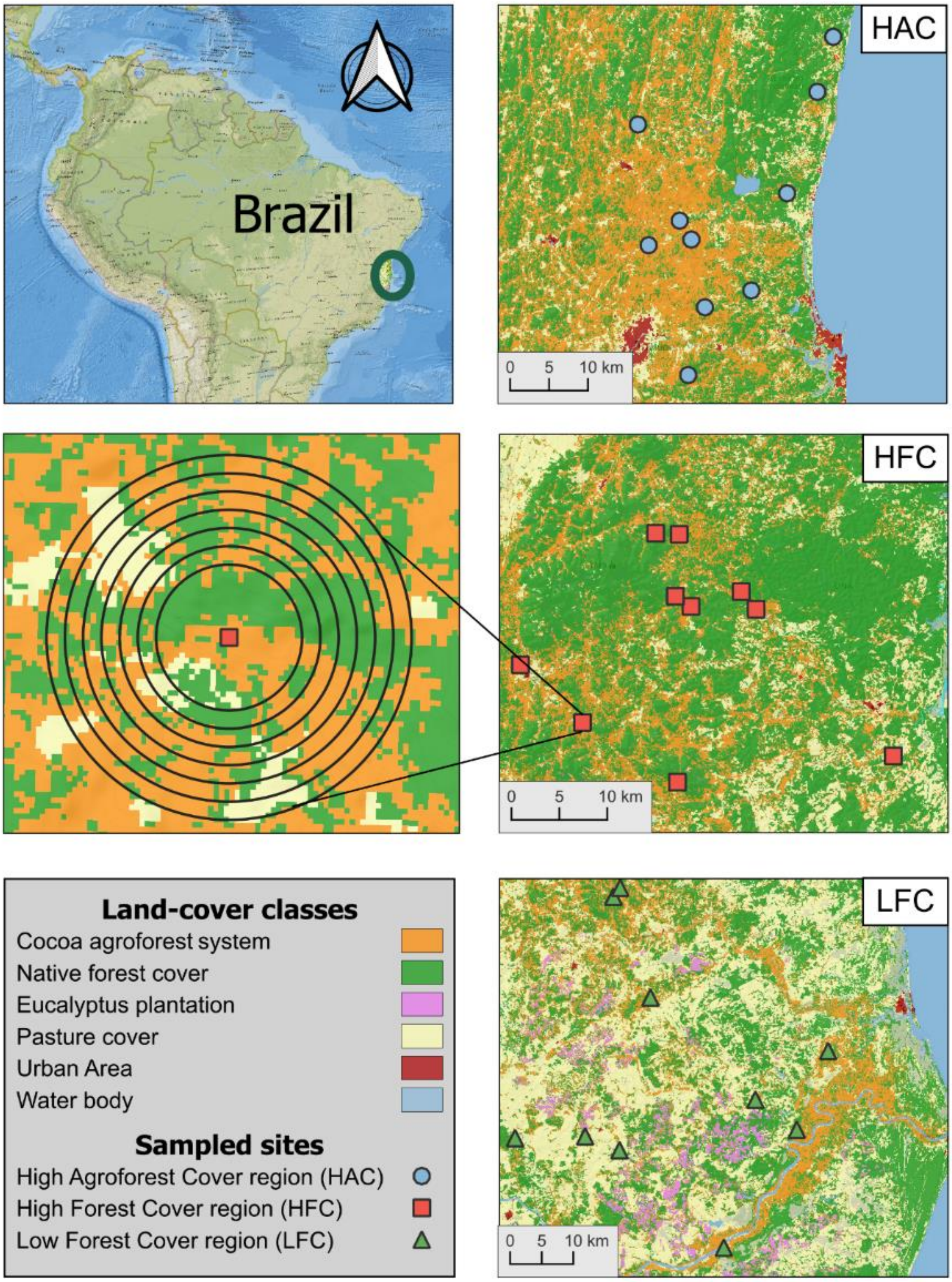

Figure 1. Sampling sites in the state of Bahia, southern Brazil, showing 30 shaded cocoa sites (blue dots, red squares and green triangles) in three regions with different land use patterns. The northernmost region (HAC) has moderate forest cover and a high

cover of cocoa agroforests. The central region (HFC) features high forest cover and moderate amount of cocoa agroforests. The southernmost region (LFC) is dominated by pastures, eucalyptus plantations, and reduced amount of native forests and cocoa agroforests. Additionally, an enlarged schematic of a sampling site illustrating the seven buffer sizes, with radii ranging from 400 to 1000 m. These buffers were used to evaluate the most relevant spatial scales of the landscape predictors in relation to the beta diversity metrics of amphibian and reptile communities.

Landscape predictors

To assess the influence of landscape predictors on taxonomic, functional, and phylogenetic beta diversity, we used two variables related to land cover composition: native forest and pasture percentages. Landscape metrics were calculated using a patch-landscape approach (Fahrig 2013) within circular buffers (400–1000 m radius) around each site. The selected scales correspond to the scale-of-effect values identified in a previous study in the same regions (Appendix S1), which found the strongest associations between these landscape predictors and herpetofaunal species richness (Cervantes-López et al. 2025). For detailed information on how these landscape metrics were calculated, including buffer sizes, land cover classifications, and GIS procedures, see Cervantes-López et al. (2025).

Local predictors

We selected two local predictors, the number of shade trees and canopy cover, related to the complexity of vertical vegetation structure within cocoa agroforest systems, to assess whether differences in these structural predictors between pairs of sites influence the beta diversity patterns of amphibian and reptile communities. For this, we first established three 50 m × 3 m parallel plots at each site, spaced 20 m apart. Within these plots, we counted the number of shade trees with a diameter at breast height (DBH) of at least 10 cm, including both native and exotic species. In addition, the average canopy cover was calculated in the initial, middle and final sections of each plot (Tichý 2016) using a Motorola E7 smartphone with a hemispherical fisheye lens and the Gap Light Analysis (GLAMA) mobile application. All images were taken at a height of 4 meters, focusing only on the canopy of shade trees and excluding the canopy of cocoa trees.

Amphibian and reptile sampling

The sampling of amphibian and reptile species was conducted in two seasons: January-April and September-December 2023. Using the Visual Encounter Survey method (Doan 2003), two researchers searched for herpetofauna in all microhabitats up to a height of 2 a m within cocoa agroforests. The 30 agroforests were sampled for two days in each season, with six-hour sessions split between day (10:00-13:00) and night (18:00-21:00), totaling 24 hours of sampling effort per site (2 seasons x 2 days x 6 hours). Specimens were identified with field guides for amphibians (Haddad et al. 2013; Freitas 2015) and reptiles (Argôlo 2004; Freitas 2015). Unidentified specimens were collected for latter identification by experts and deposited in the Zoology Museum of the Universidade Estadual de Santa Cruz (UESC). Taxonomy followed Frost (2024) for amphibians and Uetz and Stylianou (Uetz and Stylianou 2018) for reptiles.

Species traits and phylogenetic tree

To estimate the beta functional diversity of all species recorded, we compiled ecological traits of amphibians (Moura et al. 2017; Oliveira et al. 2017; Liedtke et al. 2022) and reptiles (Moura et al. 2017) from the available literature. The ecological traits selected were included body size and biomass as numerical variables, as well as activity period, microhabitat preference, and reproductive strategy as categorical variables. However, in the case of amphibians, biomass was excluded due to its high correlation with body size (r = 0.8). The traits chosen provide valuable information on life histories, interactions with the environment, and on the ecological roles that species may play (Cortéz-Gómez et al. 2015). For a detailed description of each trait and explanations on their ecological importance, see Cervantes-López et al. (2025).

For beta phylogenetic diversity, we estimated the phylogenetic relationships among species of amphibians (Jetz and Pyron 2018) and reptiles (Tonini et al. 2016) by using available phylogenetic trees. For amphibians, we employed the best available tree (Jetz and Pyron 2018), while for reptiles, we needed to construct a consensus tree. To achieve this, a Maximum Credibility Clade (MCC) consensus tree was generated using the *mcc* function from the ‘phangorn’ package (Schliep et al. 2017), based on 10,000 sampled phylogenies. Furthermore, for newly described species not yet incorporated into these phylogenies—such as the frogs *Bahius bilineatus*, *Phyllodytes magnus*, *Pristimantis* sp., and *Vitreorana baliomma*— we used the evolutionary age of their closest congeners (Ouchi-Melo et al. 2018).

Taxonomic, functional and phylogenetic beta diversity

First, we assessed the sampling completeness of the amphibian and reptile communities using the sample coverage estimator proposed by Chao and Jost (2012), implemented in the R package "iNEXT3D" (Chao et al. 2021). Sample coverage is defined as the proportion of the total number of individuals in a community that belong to the species represented in the sample (Chao and Jost 2012). Values close to 1 indicate high completeness, meaning that few undetected species are expected. For amphibians, sample coverage values at each site ranged from 94% to 100%, indicating that our sampling effort was sufficient and that the results are reliable for this taxon. In contrast, reptile coverage exhibited greater variability, with values ranging from 61% to 98%. (Appendix S2). After estimating species richness, we detected that the observed richness values were highly correlated ($r = 0.78$, $p < 0.005$) with the estimated values for reptile species, so we decided to use the observed values for the beta diversity calculations, following the approach adopted in (Bassetto et al. 2024).

To assess the taxonomic, functional, and phylogenetic beta diversity of amphibian and reptile communities, we used Sorensen's dissimilarity index based on a species incidence matrix, which ranges from 0 (high compositional similarity) to 1 (high compositional dissimilarity). Beta diversity was calculated between pairs of cocoa sites sampled within each of the three regions using the *beta* function from the 'BAT - Biodiversity Assessment Tools' package (Cardoso et al. 2014) in R. This function estimates Sorensen's beta diversity, considering not only species identity (i.e., taxonomic diversity) but also functional and phylogenetic components. The phylogenetic beta diversity was calculated using a phylogenetic tree, while the functional beta diversity was generated from trait distance matrices based on Gower's distance coefficient (Ricotta et al. 2020).

Data analysis

We assessed whether differences in the dispersion of taxonomic, functional, and phylogenetic beta diversity existed among the regions: High Agroforest Cover (HAC), High Forest Cover (HFC), and Low Forest Cover (LFC), using the *betadisper* function from the 'vegan' package (Oksanen et al. 2024), which computes the average distance of sites to their group centroid in multivariate space. To test for significant differences in dispersion among regions, we applied the *permutest* function with 9999 permutations. This approach focuses on differences in the multivariate dispersion of communities, irrespective of their position in multivariate space. A higher mean distance to centroid indicates greater heterogeneity within a group, reflecting higher beta diversity (Anderson et al. 2006).

We constructed pairwise dissimilarity matrices for each predictor variable using Euclidean distances, including landscape predictors (Δ native forest cover and Δ pasture cover), local predictors (Δ number of shade trees and Δ canopy cover), and spatial distance (Δ distance among sites), using the *dist* function from the ‘vegan’ package (Oksanen et al. 2024). Prior to the analysis, we assessed collinearity among predictor variables separately for each region, taxonomic group, and diversity dimension using Pearson correlation matrices. Although one pair of variables reached a correlation coefficient of 0.7, we did not consider it indicative of problematic collinearity, as all other values remained below this threshold (Appendix S3). Then, we conducted Multiple Regression on distance Matrices (MRM) using the *MRM* function from the ‘ecodist’ package (Goslee and Urban 2007), to assess the relationships between the taxonomic, functional, and phylogenetic beta diversity matrices and the Euclidean distance matrices of each predictor. The significance of regression coefficients was evaluated using a permutation test with 9999 permutations.

Results

Patterns of beta diversity across regions

We detected 74 amphibian species and 40 reptile species across 30 shaded cocoa agroforests. The same number of amphibian species (49) was observed in the High Agroforestry Cover (HAC) and High Forest Cover (HFC) regions, while the Low Forest Cover (LFC) region showed the highest richness, with 62 species. For reptiles, we observed 28, 24, and 25 species in HAC, HFC, and LFC, respectively (Appendix S4).

Overall, Sorensen's index values for taxonomic, functional, and phylogenetic beta diversity of amphibians and reptiles were low (Figure 2). In amphibians, the highest mean values of beta diversity across all diversity dimensions were observed in the LFC region, followed by the HFC region, with the lowest values recorded in HAC (Figure 2). For reptiles, the highest mean beta diversity values were observed in the HFC region, followed by the LFC region (Figure 2). Furthermore, for both taxa, multivariate dispersion did not differ significantly among regions for any beta diversity dimension (Figure 3; Table 1).

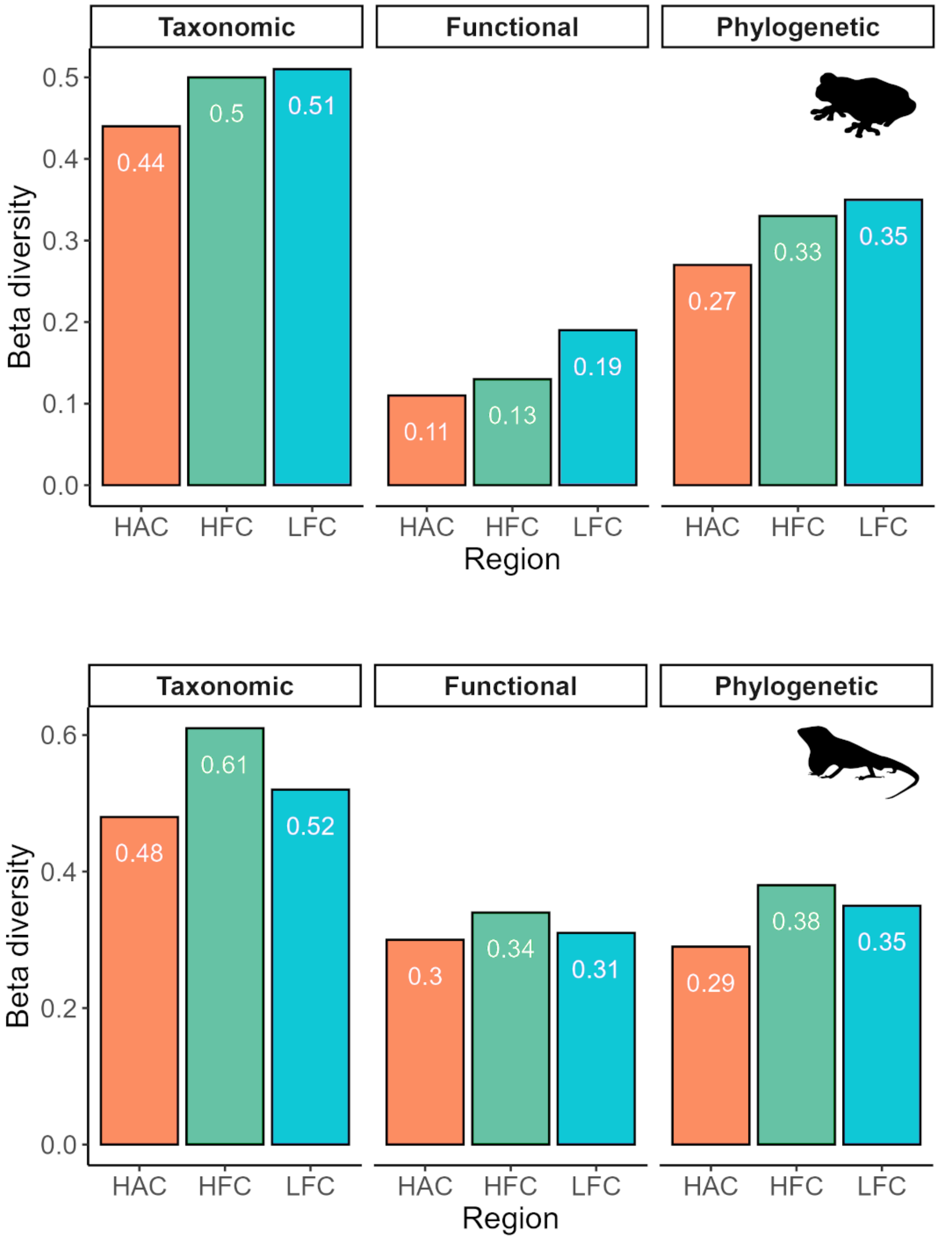

Figure 2. Taxonomic, functional, and phylogenetic beta diversity of amphibian and reptile species among cocoa agroforests located in three regions with contrasting land uses. The numbers within each bar represent the mean Sorensen index between cocoa site pairs in each study region: High Agroforest Cover (HAC), High Forest Cover (HFC), and Low Forest Cover (LFC).

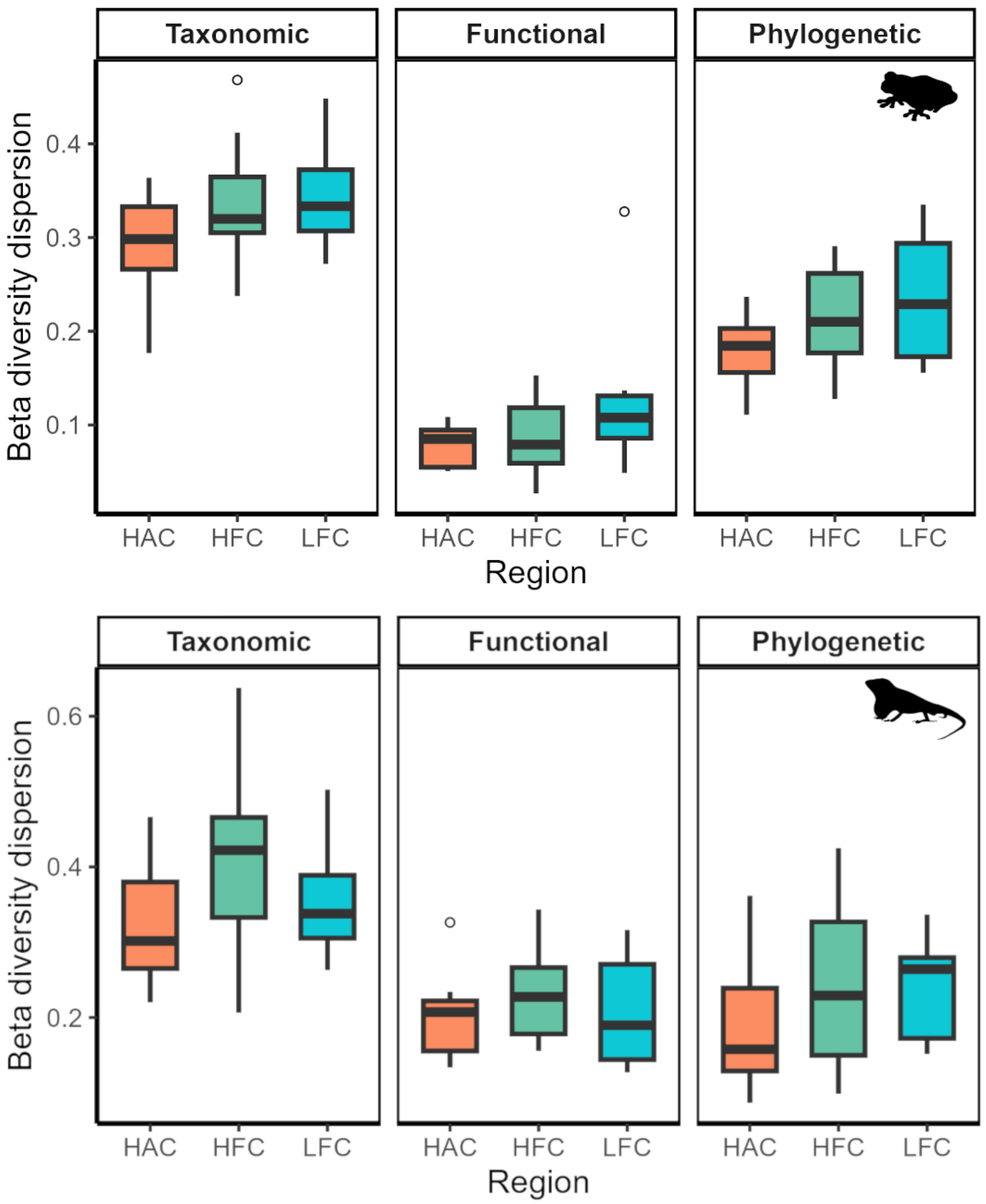

Figure 3. Boxplots showing the dispersion of taxonomic, functional, and phylogenetic beta diversity of amphibian and reptiles communities in the cocoa agroforests across three regions with contrasting land uses: High Agroforest Cover (HAC), High Forest Cover (HFC), and Low Forest Cover (LFC). Dispersion is represented by the distance of each site to the group centroid in multivariate space. Circles indicate outliers.

Table 1. Results of PERMDISP analyses, presenting the mean distances of sites to their respective group centroids for beta diversity among regions, along with the tests of homogeneity of multivariate dispersions. The abbreviations for the regions are: HAC = High Agroforest Cover, HFC = High Forest Cover, LFC = Low Forest Cover.

Amphibians	**Average distance to median in each region**			**Sum of square**	**Mean square**	**F value**	**P-value**
Dimensions of beta diversity	**HAC**	**HFC**	**LFC**				
Taxonomic	0.29	0.34	0.34	0.02	0.01	2.31	0.12
Functional	0.08	0.08	0.12	0.01	0.01	2.14	0.11
Phylogenetic	0.18	0.22	0.23	0.02	0.01	2.63	0.08

Reptiles	**Average distance to median in each region**			**Sum of square**	**Mean square**	**F value**	**P-value**
Dimensions of beta diversity	**HAC**	**HFC**	**LFC**				
Taxonomic	0.32	0.41	0.36	0.04	0.02	2.31	0.12
Functional	0.20	0.23	0.21	0.01	0.00	0.65	0.52
Phylogenetic	0.19	0.25	0.24	0.02	0.01	0.98	0.38

Effect of environmental differences and geographical distance on multiple facets of beta diversity in amphibians and reptiles

The MRM analysis results for amphibians in the region with the highest agroforest cover (HAC) showed that beta diversity across all dimensions was negatively associated with increasing differences in the number of shade trees (Fig. 4a, c, d), whereas differences in canopy cover negatively affected only taxonomic beta diversity (Fig. 4b). In contrast, in the region with the highest forest cover (HFC), taxonomic beta diversity increased among sites with greater differences in the number of shade trees (Fig. 4e). Additionally, functional and phylogenetic beta diversity increased among sites with greater differences in pasture cover (Fig. 4f-g). Finally, in the most deforested region (LFC), only taxonomic and phylogenetic beta diversity increased among the most geographically isolated sites (Fig. 4h-i; Table 2).

In reptiles of the HAC region, taxonomic and phylogenetic beta diversity were significantly influenced by differences in canopy cover (Fig. 4j-k); however, for phylogenetic beta diversity, the P-value was only marginally significant (Table 2). Within the HFC region, taxonomic beta diversity was positively associated with greater differences in forest cover, also with marginal significance (Fig. 4l; Table 2), while increasing geographic distance between sites contributed to higher phylogenetic beta diversity (Fig. 4m). Finally, in the LFC region, only differences in pasture cover and geographical distance affected phylogenetic beta diversity: pasture cover was negatively associated, while spatial distance among sites had a positive effect (Fig. 4n-o, Table 2).

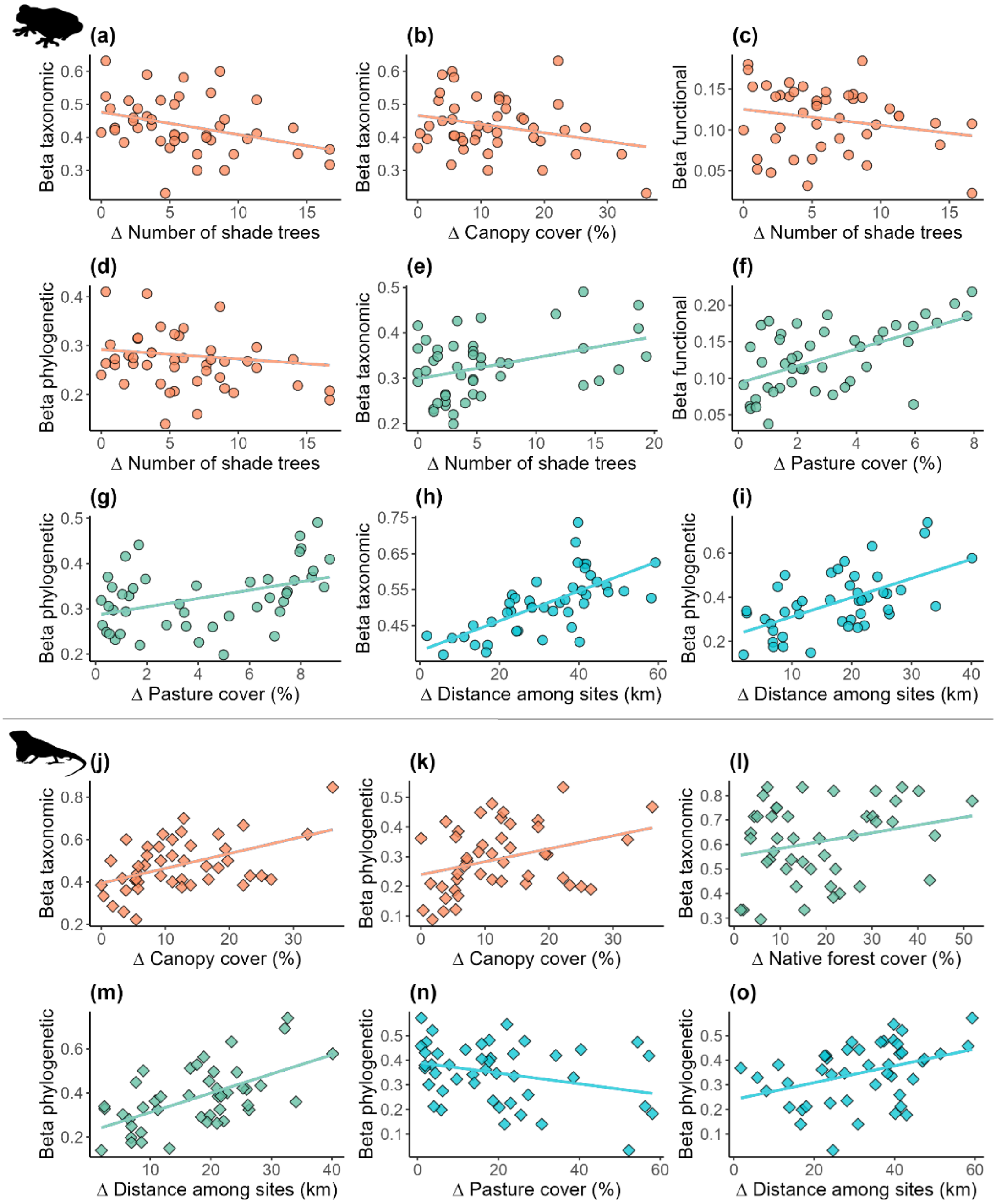

Figure 4. Effect of differences (Δ) in local and landscape predictors and geographical distance among sites on taxonomic, functional, and phylogenetic beta diversity of amphibian (circle symbols) and reptile (diamond symbols) communities sampled in shade cocoa agroforest. Symbol colors represent the sampled regions: coral for High Agroforest Cover (HAC), light green for High Forest Cover (HFC), and light blue for Low Forest Cover (LFC). Solid lines represent model-based trend lines derived from Multiple Regression on distance Matrices (MRM).

Table 2. Beta regression coefficients and P-values from MRM analyses assessing the influence of differences in local and landscape environmental predictors and spatial distance, as well as geographical distance between sites, on taxonomic, functional, and phylogenetic beta diversity of amphibians and reptiles across three regions with contrasting land-use contexts. Significant results ($P \leq 0.05$) are shown in bold. The abbreviations for the regions are: HAC = High Agroforest Cover, HFC = High Forest Cover, LFC = Low Forest Cover.

Amphibians beta diversity						
Region HAC	**Taxonomic**		**Functional**		**Phylogenetic**	
Predictor	**Coefficient**	**P-value**	**Coefficient**	**P-value**	**Coefficient**	**P-value**
Δ Native forest cover	0.075	0.358	0.053	0.183	0.092	0.089
Δ Pasture cover	0.919	0.118	-0.014	0.940	0.631	0.115
Δ Number of shade trees	**-0.010**	**0.005**	**-0.004**	**0.035**	**-0.006**	**0.011**
Δ Canopy cover	**-0.004**	**0.027**	-0.001	0.155	-0.002	0.077
Δ Distance among sites	0.002	0.200	0.001	0.216	0.001	0.404
Region HFC	**Taxonomic**		**Functional**		**Phylogenetic**	
Predictor	**Coefficient**	**P-value**	**Coefficient**	**P-value**	**Coefficient**	**P-value**
Δ Native forest cover	-0.070	0.695	0.106	0.097	0.050	0.721
Δ Pasture cover	0.870	0.070	**1.042**	**0.010**	**0.836**	**0.008**
Δ Number of shade trees	**0.008**	**0.046**	0.000	0.945	0.004	0.118
Δ Canopy cover	-0.002	0.658	0.000	0.804	0.001	0.705
Δ Distance among sites	0.001	0.537	0.001	0.378	0.002	0.190
Region LFC	**Taxonomic**		**Functional**		**Phylogenetic**	
Predictor	**Coefficient**	**P-value**	**Coefficient**	**P-value**	**Coefficient**	**P-value**
Δ Native forest cover	-0.048	0.526	-0.156	0.288	-0.026	0.795
Δ Pasture cover	-0.036	0.559	-0.072	0.426	-0.033	0.738
Δ Number of shade trees	-0.005	0.258	-0.006	0.535	-0.005	0.515
Δ Canopy cover	0.000	0.944	0.005	0.215	0.002	0.396
Δ Distance among sites	**0.004**	**<0.001**	0.002	0.079	**0.003**	**0.011**
Reptiles beta diversity						
Region HAC	**Taxonomic**		**Functional**		**Phylogenetic**	
Predictor	**Coefficient**	**P-value**	**Coefficient**	**P-value**	**Coefficient**	**P-value**
Δ Native forest cover	-0.031	0.801	**0.488**	**0.054**	0.064	0.713
Δ Pasture cover	-0.510	0.235	-1.822	0.226	-0.208	0.131
Δ Number of shade trees	0.002	0.784	-0.007	0.241	-0.001	0.906
Δ Canopy cover	**0.009**	**0.003**	0.005	0.382	-0.001	0.852
Δ Distance among sites	0.000	0.880	0.005	0.108	0.002	0.192
Region HFC	**Taxonomic**		**Functional**		**Phylogenetic**	
Predictor	**Coefficient**	**P-value**	**Coefficient**	**P-value**	**Coefficient**	**P-value**
Δ Native forest cover	-0.115	0.215	0.046	0.791	0.056	0.618
Δ Pasture cover	0.439	0.177	-1.040	0.298	-0.136	0.250
Δ Number of shade trees	0.002	0.562	-0.002	0.568	0.006	0.484
Δ Canopy cover	0.001	0.572	0.000	0.981	0	0.913
Δ Distance among sites	-0.001	0.616	0.002	0.413	0	0.732

Region LFC	Taxonomic		Functional		Phylogenetic	
Predictor	**Coefficient**	**P-value**	**Coefficient**	**P-value**	**Coefficient**	**P-value**
Δ Native forest cover	-0.054	0.695	0.262	0.203	-0.064	0.65
Δ Pasture cover	-0.542	0.293	-2.119	0.141	**-0.210**	**0.04**
Δ Number of shade trees	-0.003	0.641	-0.008	0.212	0.000	0.95
Δ Canopy cover	**0.006**	**0.055**	0.003	0.621	-0.001	0.82
Δ Distance among sites	0.000	0.861	**0.008**	**0.005**	**0.004**	**0.02**

Discussion

In this study, we examined the patterns and environmental drivers of taxonomic, functional, and phylogenetic beta diversity of amphibians and reptiles in shaded cocoa agroforests across three regions with contrasting land-use contexts in southern Brazil. Overall, beta diversity was relatively low across all dimensions and taxa, with amphibians showing peak values in the most deforested region and reptiles in the most forested region. The cocoa-dominated region consistently exhibited the lowest beta diversity in both groups. These results indicate that changes in species composition among communities in shaded cocoa agroforest varies across regions and biodiversity dimensions, suggesting that different ecological mechanisms may be shaping patterns of species replacement. Moreover, environmental and spatial predictors were associated with both increases and decreases in beta diversity, depending on the region, taxonomic group, and dimension considered. In the following sections, we discuss how these patterns relate to environmental heterogeneity, dispersal limitation, and landscape structure.

Although differences in beta diversity among regions were not statistically significant, the cocoa-dominated region (HAC) consistently showed the lowest taxonomic, functional, and phylogenetic beta diversity for both amphibians and reptiles. In contrast, amphibian beta diversity peaked in the most forested (HFC) and most deforested (LFC) regions, while reptiles showed highest values in HFC. These patterns suggest that different ecological processes influence community dissimilarity across regions: environmental filtering in HFC, dispersal limitation in LFC, and biotic homogenization in HAC. In this latter region, the structural similarity among cocoa agroforest and their dominance in the landscape likely reduce environmental heterogeneity and the strength of ecological filters, favoring a limited set of disturbance-tolerant species (Tscharntke et al. 2012; Gámez-Virués et al. 2015). For example, Faria et al. (2007) reported that in regions with few forest fragments and large areas occupied by cocoa agroforests—as in the case of HAC—communities tend to be impoverished and dominated by generalist species, which can reduce beta diversity compared to more forested regions such as HFC. These findings highlight the importance of maintaining habitat complexity and connectivity to avoid the loss of taxonomic, functional, and phylogenetic differentiation among communities in more homogeneous regions

Regarding the effects that environmental and distance predictors could have on the different dimensions of beta diversity in amphibians, in the HAC region, beta diversity—taxonomic, functional, and phylogenetic—decreased with increasing differences in shade tree abundance, and taxonomic beta diversity also declined with variation in canopy cover. This suggests that differences in vegetation structure between cocoa agroforest are not sufficient to generate meaningful environmental heterogeneity, but instead result in uniformly simplified habitats dominated by generalist species with similar ecological traits and close evolutionary relationships (Pineda and Halffter 2004; Lara-Tufiño et al. 2019). A similar pattern was reported by Murrieta-Galindo et al. (2013), who observed that, even in structurally complex agroforests like shade coffee agroforest, the presence of amphibian species was shaped not only by local habitat structure but also by the surrounding landscape matrix. More recently, Juárez-Ramírez et al. (2024) showed that these agroforests supported only a subset of the forest amphibian community, with sensitive and threatened species largely absent, indicating strong environmental filtering. These findings underscore that in HAC, even agroforests with higher tree density may fail to support forest-dependent species if the broader landscape remains homogeneous and fragmented (Faria et al. 2007).

On the other hand, in HFC for amphibians, taxonomic beta diversity increased with variation in shade tree abundance, while functional and phylogenetic beta diversity rose with differences in pasture cover. These patterns suggest that both local and landscape-level structural heterogeneity promote community differentiation through environmental filtering. Locally, variation in shade tree abundance likely generates microhabitat gradients in humidity, light, and structure that affect species distributions (Wanger et al. 2010; Teixeira et al. 2015; Juárez-Ramírez et al. 2024). For instance, Juárez-Ramírez et al. (2024) highlighted that greater tree density and diversity within forest habitats favors greater availability of food resources for various amphibian species that use these microhabitats. This result reflects how variation in these local structural characteristics can reinforce small-scale environmental filtering mechanisms, promoting greater community differentiation and, consequently, an increase in beta diversity of species and lineages between environments. At the landscape scale, greater pasture cover differences were linked to higher functional and phylogenetic beta diversity, likely because pastures introduce structural and microclimatic contrasts that act as ecological filters. Such filters may favor species with traits suited to drier and more exposed environments (Da Cunha Bitar et al. 2015; Hernández-Ordóñez et al. 2019; Almeida-Gomes et al. 2019), such as larger body size, higher desiccation tolerance. Examples of some of these species in our study are *Rhinella crucifer*, *Boana faber*, *B. albomarginata*, *Trachycephalus mesophaeus*, *Leptodactylus latrans*. This aligns with Lourenço-de-Moraes et al. (2020), who showed that amphibian distributions are strongly shaped by traits like body size and habitat use, with species adapted to open areas having broader ranges. Thus, trait-based filtering likely contributes to the observed increase in functional and phylogenetic dissimilarity across heterogeneous pasture landscapes.

Within the LFC region, increased geographic distance between sites was associated with higher taxonomic and phylogenetic beta diversity in amphibians This pattern is probably due to limited dispersal of amphibians species (Landeiro et al. 2014; Knauth et al. 2019). Amphibians generally have low dispersal ability due to physiological constraints such as permeable skin and strong dependence on moist habitats, which hinder movement across open, dry areas (Almeida-Gomes and Rocha 2014; Ribeiro et al. 2017; Lourenço-de-Moraes et al. 2020; Garey et al. 2023). As a result, species with limited locomotion, like *Allophryne relicta*, *Chiasmocleis crucis*, *Pristimantis vinhai*, and *Haddadus binotatus* or *Proceratophrys schirchi* may become restricted to isolated sites, while more tolerant and widespread species—such as *Leptodactylus mystacinus*, *Leptodactylus latrans* and *Rhinella crucifer*—can move across fragmented landscapes. This spatial segregation caused by limited dispersal promotes not only variation in species composition, but also phylogenetic dissimilarity among communities, as distinct evolutionary lineages become unevenly distributed across the landscape (Da Silva et al. 2014; Wang et al. 2022). This is particularly relevant given that many low-dispersal species belong to distinct evolutionary lineages, so their restricted distribution across the landscape contributes directly to higher phylogenetic beta diversity.

In the HAC region, reptile taxonomic and marginally phylogenetic beta diversity were positively associated with differences in canopy cover between agroforest sites. This pattern likely reflects the strong sensitivity of reptiles to microclimatic variation, as species with contrasting thermoregulatory strategies—such as heliothermic lizards and forest-dwelling snakes—respond differently to canopy openness (Moura et al. 2017; Palmeirim et al. 2017). Canopy cover shapes key environmental conditions—light, humidity, and temperature—which act as filters selecting for species with specific physiological tolerances (Peña-Joya et al. 2020; Marques Peixoto et al. 2020). As shown in other tropical landscapes, open areas tend to favor thermophilic generalists, while shaded environments support forest specialists (Urbina-Cardona et al. 2006; Carvajal-Cogollo and Urbina-Cardona 2015). In our system, sun-exposed sites harbored species such as *Ameiva ameiva*, *Tropidurus torquatus*, *Salvator merianae*, and *Kentropix calcarata*, whereas closed-canopy areas supported species like *Coleodactylus meridionalis*, *Enyalius catenatus*, and *Polychrus marmoratus* (Tozetti et al. 2017). This structural heterogeneity likely promotes turnover in both taxonomic and phylogenetic composition across sites.

For reptiles in the HFC region, taxonomic beta diversity increased with variation in forest cover, although the effect was marginally significant. This suggests that species with differing degrees of specialization to native forests and cocoa agroforest may respond differently to changes in habitat availability. Similar patterns have been observed in birds in Taiwan (Shih et al. 2024) and ant communities in Brazil (Martins et al. 2022), where variation in forest cover promoted species sorting according to habitat requirements. These findings highlight the role of environmental heterogeneity in shaping community composition, as greater variation in forest cover can enhance dissimilarity among sites. In such landscapes, a broader spectrum of ecological conditions and resources may also support the coexistence of both generalist and specialist species. Meanwhile, phylogenetic beta diversity increased with greater geographic distance between sites, indicating spatial segregation among evolutionary lineages. This pattern likely reflects the limited dispersal capacity and strong habitat fidelity of many forest-specialist species (Morante-Filho et al. 2016), including several reptiles known for their small home ranges and restricted movement across disturbed habitats (Meiri et al. 2018). As distance among sites increases, movement across agroforest patches becomes less likely, species such as *Diploglossus fasciatus*, *Gymnodactylus darwinii*, *Corallus hortulanus*, *Leposoma scincoides*, *Coleodactylus meridionalis*, and *Oxyrhopus petolarius*, which are categorized by the IUCN as forest-dependent. Also, these species also belong to phylogenetically distinct clades, reinforcing the potential for spatial segregation of evolutionary lineages across fragmented landscapes.

In the LFC region, we found contrasting spatial patterns in reptile phylogenetic beta diversity: while greater differences in pasture cover were linked to a decrease, increased geographic distance promoted higher dissimilarity. These results suggest that different mechanisms operate at local and broader spatial scales. At the local scale, variation in pasture may drive biotic homogenization by favoring generalist species from a few widespread clades (Cavalheri et al. 2015), possibly amplified by a spillover of open-habitat species into cocoa agroforests (Arce-Peña et al. 2022; Vargas-Cárdenas et al. 2025). These generalist species, often closely related, may compete with or displace forest specialists, leading to reduced beta diversity among sites. Studies have shown that habitat disturbance promotes generalist proliferation and simplifies community composition by excluding more sensitive species (Nordberg and Schwarzkopf 2019; Cuadrado et al. 2023). Ultimately, the loss of forest cover and structural simplification of the landscape likely reduce the persistence of forest-dependent lineages, resulting in phylogenetic clustering (Leal-Santos et al. 2024; Cervantes-López et al. 2025). Conversely, increased geographic distance between sites also contributed to higher phylogenetic beta diversity, likely due to limited dispersal of forest-associated clades with low vagility or strong habitat fidelity (Cavalheri et al. 2015; Leal-Santos et al. 2024). However, in this highly deforested landscape, dispersal constraints are further intensified by the presence of extensive pastures, which not only lack vegetative cover but also impose thermal stress and exposure to pesticides and predators (Nowakowski et al. 2018b; Leal-Santos et al. 2024). These additional barriers reinforce the spatial segregation of lineages, enhancing phylogenetic differentiation across distant sites.

Conclusions

The findings of this study reveal that the different dimensions of beta diversity in amphibians and reptiles inhabiting shaded cocoa agroforests can be influenced by landscape context, the heterogeneity of local and landscape-level environmental conditions, as well as geographic distance between sites. Moreover, the influence of these predictors varies depending on the dimension of diversity considered, the region in question, or the taxonomic group analyzed.

As agricultural expansion continues to transform tropical regions into increasingly fragmented landscapes (Wong 2024), this study highlights the importance of incorporating the conservation of herpetofaunal beta diversity into shaded agroforest systems and broader land-use planning. Recognizing the spatial and ecological drivers of community differentiation is essential for conserving biodiversity (Socolar et al. 2016)—particularly amphibian and reptile communities that harbor high taxonomic, functional, and phylogenetic diversity in the Atlantic Forest (Da Silva et al. 2014; Leão-Pires et al. 2018; Cervantes-López et al. 2025)—in human-modified environments. In this context, maximizing conservation outcomes will require strategies tailored to the divergent patterns observed in each region, applying landscape-specific approaches to effectively support herpetofaunal diversity.

First, in the region with high coverage of shaded cocoa agroforests, our results indicate that improving only the local vegetation structure is not sufficient to maintain the differentiation of amphibian communities across sites. For this group, it is essential to increase landscape heterogeneity through the conservation and restoration of native forest fragments, which can promote the differentiation of species with distinct functional traits and evolutionary lineages, as well as facilitate dispersal and reduce homogenizing effects within agroforestry matrices. In contrast, for reptiles, we observed that local differences in canopy cover were indeed associated with higher beta diversity, highlighting the importance of promoting greater structural complexity within cocoa agroforests.

In the region with high forest cover, our results indicate that enhancing local structural complexity is key to maintaining amphibian community differentiation among sites. However, it is also critical to preserve heterogeneity at the landscape scale—particularly variation in pasture cover and connectivity among forest fragments—which can promote the coexistence of species with distinct ecological traits and evolutionary lineages. For reptiles, beta diversity was influenced by both local and spatial factors, highlighting the importance of maintaining varied forest cover and ensuring functional connectivity across sites to foster phylogenetic differentiation in forest-dominated landscapes.

In the region most dominated by pastures and heavily affected by deforestation, conserving and restoring native forest fragments is essential for promoting functional connectivity between habitats and facilitating the exchange of amphibian and reptile species with diverse evolutionary histories. Furthermore, our findings suggest that the expansion of homogeneous pastures may intensify environmental filtering and favor the dominance of a few tolerant reptile lineages. Avoiding the spread of these open areas and maintaining a mosaic with higher forest cover is crucial to safeguarding the evolutionary diversity of herpetofauna in heavily deforested landscapes.

Taken together, these findings highlight that shaded cocoa agroforest can play an important role in biodiversity conservation if they are properly managed and embedded within functionally connected landscapes. Assessing multiple facets of the beta diversity provide a powerful tool to identify the processes structuring communities and to design conservation strategies necessary for the conservation of vertebrate groups highly threatened by the loss and degradation of their natural habitat.

CRediT authorship contribution statement

M.J. Cervantes-López coordinated sampling activities, managed data collection and organization, wrote grant proposals, designed databases, created visual figures, conducted data analyses, and drafted the manuscript. J.C. Morante-Filho supervised the research process, assisted in securing funding, and thoroughly reviewed all manuscript drafts, providing valuable insights and suggestions.

Declaration of Competing Interest

The authors confirm that they have no recognized financial conflicts or personal relationships that may have influenced the findings presented in this paper.

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Supporting information

Patterns and predictors of taxonomic, functional and phylogenetic beta diversity of amphibian and reptile communities in shaded cocoa agroforest

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Appendix S1. Landscape scale effect

Table S1. Summary of the relationships between forest and pasture cover and the taxonomic, functional, and phylogenetic richness of the diversity of amphibians and reptiles evaluated across multiple buffer sizes within cocoa agroforest systems. The buffer radius with the highest explanatory power (i.e., the greatest R² value) is marked in bold.

Response variable	Landscape metric	Buffer size (m)	Amphibians		Reptiles	
			R^2	p-value	R^2	p-value
Taxonomic richness	Native forest cover	400	0.10	0.09	0.08	0.13
		500	0.11	0.07	0.11	0.08
		600	0.13	0.05	0.13	0.05
		700	0.15	0.04	0.15	0.04
		800	**0.16**	**0.03**	0.16	0.03
		900	0.15	0.03	0.17	0.02
		1000	0.15	0.04	**0.17**	**0.02**
Functional richness	Native forest cover	400	0.01	0.59	0.04	0.30
		500	0.01	0.53	0.05	0.25
		600	0.02	0.46	0.06	0.21
		700	0.03	0.39	0.07	0.17
		800	0.03	0.36	**0.07**	**0.16**
		900	0.03	0.36	0.07	0.16
		1000	**0.03**	**0.35**	0.07	0.17

Phylogenetic richness	Native forest cover	400	0.10	0.10	0.06	0.20
		500	0.11	0.07	0.08	0.12
		600	0.13	0.05	0.11	0.08
		700	0.15	0.03	0.12	0.06
		800	**0.16**	**0.03**	0.13	0.05
		900	0.16	0.03	0.15	0.04
		1000	0.16	0.03	**0.16**	**0.03**
$^0\alpha_{taxonomic}$	Pastures cover	400	0.20	0.01	0.01	0.52
		500	0.18	0.02	**0.02**	**0.42**
		600	0.22	0.01	0.01	0.53
		700	0.27	0.00	0.01	0.66
		800	0.29	0.001	0.01	0.71
		900	0.31	0.001	0.00	0.77
		1000	**0.31**	**0.001**	0.00	0.77
$^0\alpha_{Functional}$	Pastures cover	400	0.09	0.11	0.01	0.67
		500	0.07	0.15	**0.01**	**0.55**
		600	0.08	0.12	0.01	0.63
		700	0.10	0.08	0.00	0.79
		800	**0.12**	**0.07**	0.00	0.87
		900	0.11	0.07	0.00	0.96
		1000	0.11	0.07	0.00	0.98
$^0\alpha_{Phylogenetic}$	Pastures cover	400	0.12	0.06	0.02	0.41
		500	0.10	0.08	**0.03**	**0.35**
		600	0.12	0.06	0.02	0.45
		700	0.16	0.03	0.01	0.59
		800	0.19	0.02	0.01	0.61
		900	0.20	0.01	0.01	0.62
		1000	**0.21**	**0.01**	0.01	0.60

Appendix 2. Species richness recorded in 30 shaded cocoa agroforest systems.

Table S2. Species richness of amphibians and reptiles recorded in 30 shaded cocoa agroforest systems, distributed across three regions with varying land-use contexts. Additionally, we included the sample coverage for each agroforests system, which estimates the proportion of the total community abundance represented by the sampled species, following the method of Chao and Jost 2012. Regions are classified as follows: HAC - High Agroforest Cover, HFC - High Forest Cover, and LFC - Low Forest Cover.

Region	**Code site**	**Amphibians**		**Reptiles**	
		Species richness	**Sample coverage**	**Species richness**	**Sample coverage**
HAC	I10	22	0.97	14	0.83
	I11	20	0.95	7	0.95
	I12	21	0.96	10	0.94
	I13	21	0.95	7	0.92
	I14	19	0.98	13	0.87
	I15	24	0.99	14	0.85
	I16	15	0.99	11	0.89
	I17	22	0.97	9	0.80
	I4	18	0.98	6	0.82
	I8	18	0.99	6	0.97
HFC	U1	14	0.99	4	0.86
	U11	21	0.97	8	0.76
	U12	15	0.95	6	0.66
	U13	26	0.96	3	0.76
	U14	9	0.99	6	0.96
	U15	20	0.94	8	0.67
	U16	14	0.98	5	0.77
	U17	16	0.97	8	0.61
	U3	15	1.00	9	0.77
	U7	22	0.97	8	0.81
LFC	B13	21	0.96	6	0.65
	B14	22	0.96	11	0.87
	B15	16	0.97	9	0.98
	B16	22	0.99	8	0.77
	B18	16	0.98	5	0.93
	B19	21	0.96	7	0.96
	B20	19	0.98	9	0.97
	B21	25	0.98	6	0.91
	B7	32	0.97	9	0.76
	B9	23	0.95	8	0.71

Appendix S3 Pearson correlation between environmental predictors

Table S3. Pearson correlation coefficients between environmental predictors of landscape (forest cover and pasture cover) and local (number of shade trees and canopy cover) conditions used to assess their relationships with site-to-site dissimilarity in taxonomic, functional, and phylogenetic beta diversity of amphibians and reptiles across the three regions. Landscape predictors were calculated at the spatial scale (in meters) that showed the strongest effect on the richness of each diversity dimension.

Amphibians taxonomic	Forest cover (800 m)	Pasture cover (1000 m)	Number of shaded trees	Canopy cover
Forest cover (800 m)	1			
Pasture cover (1000 m)	0.04	1		
Number of shaded trees	0.50	-0.37	1	
Canopy cover	0.43	-0.10	-0.18	1

Amphibians functional	Forest cover (1000 m)	Pasture cover (800 m)	Number of shaded trees	Canopy cover
Forest cover (1000 m)	1			
Pasture cover (800 m)	-0.08	1		
Number of shaded trees	0.45	-0.41	1	
Canopy cover	0.37	-0.34	-0.18	1

Amphibians phylogenetic	Forest cover (800 m)	Pasture cover (1000 m)	Number of shaded trees	Canopy cover
Forest cover (800 m)	1			
Pasture cover (1000 m)	0.04	1		
Number of shaded trees	0.50	-0.37	1	
Canopy cover	0.43	-0.10	-0.18	1

Reptiles HAC	Forest cover (1000 m)	Pasture cover (500 m)	Number of shaded trees	Canopy cover
Forest cover (1000 m)	1			
Pasture cover (500 m)	-0.22	1		
Number of shaded trees	0.45	-0.13	1	
Canopy cover	0.37	-0.70	-0.18	1

Reptiles HFC	Forest cover (800 m)	Pasture cover (500 m)	Number of shaded trees	Canopy cover
Forest cover (800 m)	1	-0.3247487		
Pasture cover (500 m)	-0.32	1		
Number of shaded trees	0.50	-0.13	1	
Canopy cover	0.43	-0.70	-0.18	1

Reptiles LFC	Forest cover (800 m)	Pasture cover (500 m)	Number of shaded	Canopy

			trees	cover
Forest cover (800 m)	1			
Pasture cover (500 m)	-0.22	1		
Number of shaded trees	0.45	-0.13	1	
Canopy cover	0.37	-0.70	-0.18	1

Appendix 4. List of the amphibian and reptile species in 30 Shaded cocoa agroforests systems in Bahia, Brazil.

Table S4. Presence/absence matrix of amphibian (Anura and Gymnophiona) and reptile (Squamata–Ophidia and Squamata–Lacertilia) species recorded in 30 shaded cocoa agroforests distributed across three regions in Bahia state, Brazil: HAC (High Agroforest Cover), HFC (High Forest Cover), and LFC (Low Forest Cover). An “x” indicates that the species was recorded in the corresponding region, while a “–” indicates absence. Species are organized by higher taxonomic group (order and family).

ORDER (Suborder)		**Regions**		
Family	**Species**	**HAC**	**HFC**	**LFC**
ANURA				
Allophrynidae	*Allophryne relicta*	-	-	X
Aromobatidae	*Allobates olfersioides*	X	X	X
Bufonidae	*Rhinella crucifer*	X	X	X
	Rhinella granulosa	X	-	X
	Rhinella hoogmoedi	X	X	X
Centrolenidae	*Vitreorana baliomma*	-	X	X
Craugastoridae	*Haddadus binotatus*	X	X	X
Cycloramphidae	*Thoropa miliaris*	-	X	X
Eleutherodactylidae	*Adelophryne mucronatus*	X	X	-
Hemiphractidae	*Gastrotheca recava*	-	X	X
Hylidae	*Aplastodiscus ibirapitanga*	-	X	-
	Boana albomarginata	X	X	X
	Boana atlantica	X	-	X
	Boana crepitans	X	X	X
	Boana exastis	-	X	X
	Boana faber	X	X	X
	Boana pombali	X	X	X
	Boana semilineata	X	X	X
	Bokermannohyla capra	-	X	X
	Dendropsophus anceps	-	X	-
	Dendropsophus branneri	X	X	X
	Dendropsophus elegans	X	X	X
	Dendropsophus haddadi	X	X	X
	Dendropsophus minutus	-	-	X
	Dendropsophus novaisi	-	-	X

	Dendropsophus seniculus	X	-	X
	Hylomantis granulosa	-	-	X
	Itapotihyla langsdorffii	X	X	X
	Nyctimantis brunoi	-	X	X
	Ololygon argyreornata	X	X	X
	Ololygon strigilata	X	X	X
	Phyllodytes wuchereri	X	X	-
	Phyllodytes luteolus	-	X	-
	Phyllodytes magnus	X	X	-
	Phyllodytes melanomystax	X	X	-
	Phyllomedusa bahiana	-	X	X
	Phyllomedusa burmeisteri	X	X	X
	Pithecopus nordestinus	X	-	X
	Pithecopus rohdei	X	-	X
	Scinax cuspidatus	-	X	X
	Scinax eurydice	X	X	X
	Scinax fuscomarginatus	-	-	X
	Scinax fuscovarius	X	-	X
	Scinax juncae	X	X	0
	Scinax nebulosus	-	-	X
	Scinax similis	-	X	X
	Scinax x-signatus	X	X	X
	Sphaenorhynchus pauloalvini	-	-	X
	Trachycephalus mesophaeus	X	X	X
	Trachycephalus nigromaculatus	-	-	X
Leptodactylidae	*Adenomera thomei*	X	X	X
	Leptodactylus fuscus	X	-	X
	Leptodactylus latrans	X	X	X
	Leptodactylus mystaceus	X	X	X
	Leptodactylus mystacinus	X	-	-
	Leptodactylus natalensis	X	X	X
	Leptodactylus troglodytes	X	0	X
	Physalaemus camacan	X	X	X
	Physalaemus cicada	X	-	-
	Physalaemus erikae	X	X	X
Microhylidae	*Chiasmocleis cordeiroi*	X	X	X
	Chiasmocleis crucis	-	X	X
	Chiasmocleis schubarti	X	X	X
	Stereocyclops incrassatus	X	X	X
Odontophrynidae	*Macrogenioglottus alipioi*	X	-	X

	Odontophrynus carvalhoi	-	-	X
	Proceratophrys renalis	X	X	X
	Proceratophrys schirchi	-	-	X
Pipidae	*Pipa carvalhoi*	-	-	X
Strabomantidae	*Bahius bilineatus*	X	-	-
	Pristimantis paulodutrai	X	X	X
	Pristimantis sp.	X	-	-
	Pristimantis vinhai	X	X	X
Siphonopidae	*Siphonops annulatus*	-	-	X
SQUAMATA (Ophidia)				
Boidae	*Corallus hortulanus*	-	-	X
	Epicrates cenchria	-	X	-
Colubridae	*Chironius bicarinatus*	-	X	-
	Chironius exoletus	X	X	X
	Chironius fuscus	X	-	-
	Drymarchon corais	X	-	-
	Leptophis ahaetulla	X	-	-
	Oxybelis aeneus	X	-	-
Dipsadidae	*Atractus guentheri*	-	-	X
	Dipsas albifrons	-	X	X
	Dipsas catesbyi	-	-	X
	Dipsas indica	X	X	X
	Dipsas neuwiedi	X	X	-
	Dipsas variegata	X	-	X
	Erythrolamprus aesculapii	X	-	-
	Erythrolamprus miliaris	-	-	X
	Erythrolamprus reginae	X	-	-
	Imantodes cenchoa	X	X	-
	Oxyrhopus guibei	X	X	X
	Oxyrhopus petolarius	-	X	X
	Siphlophis compressus	X	-	X
	Xenopholis scalaris	X	X	-
Elapidae	*Micrurus corallinus*	-	-	X
Leptotyphlopidae	*Trilepida salgueiroi*	X	-	-
Viperidae	*Bothrops jararaca*	-	X	X
	Bothrops leucurus	-	X	-
SQUAMATA (Lacertilia)				
Anguidae	*Diploglossus fasciatus*	-	X	-
Anolidae	*Anolis fuscoauratus*	X	X	X

	Anolis punctatus	X	X	X
Gekkonidae	*Gymnodactylus darwinii*	X	X	X
Gymnophthalmidae	*Leposoma scincoides*	X	X	X
Leiosauridae	*Enyalius catenatus*	X	X	X
Phyllodactylidae	*Phyllopezus lutzae*	X	X	X
Polychrotidae	*Polychrus marmoratus*	X	-	X
Scincidae	*Psychosaura macrorhyncha*	X	-	X
Sphaerodactylidae	*Coleodactylus meridionalis*	X	X	-
	Ameiva ameiva	X	X	X
Teiidae	*Kentropyx calcarata*	X	X	X
	Salvator merianae	X	X	X
Tropiduridae	*Tropidurus torquatus*	X	X	X

General conclusion

Forest loss and degradation remain a major threat to global biodiversity, particularly for groups such as amphibians and reptiles (Bodo et al. 2021). Since conservation cannot rely solely on forest fragments, it is crucial to assess the potential of agroforests systems to mitigate the impacts of habitat loss and fragmentation (Arroyo-Rodríguez et al. 2020; Perfecto and Vandermeer 2008, 2010). In this context, shaded cocoa agroforestry systems have been recognized as valuable ecological matrices for conservation, as they offer suitable environmental conditions, key resources, and diverse microhabitats that support biodiversity (Rice and Greenberg 2000), including amphibians and reptiles (Cervantes-López et al; 2022, 2025). However, the ability of these systems to sustain biodiversity depends on factors operating at both the local and landscape scales (Cassano et al. 2014; Faria et al. 2007; Fulgence et al. 2022; Schroth and Harvey 2007).

To address this issue, this thesis combined a global and local approach: first, through a meta-analysis evaluating the capacity of agroforests systems to sustain amphibian and reptile diversity worldwide, and subsequently, through field studies in cocoa-dominated landscapes in the Atlantic Forest. In these local studies, we analyzed how landscape structure and local-scale environmental variability influence alpha and beta diversity, considering different dimensions of biodiversity. The results obtained across the three chapters of this thesis reinforce the idea that cocoa agroforests systems can play a significant role in the conservation of amphibians and reptiles, but their effectiveness varies depending on the environmental context and management practices. I

In Chapter 1, a global meta-analysis demonstrated that, in general, agroforests systems harbor lower richness and abundance of amphibians compared to native forests, while for reptiles, abundance was higher and richness was similar. However, agroforests with greater structural complexity supported more diverse reptile communities, and the presence of higher forest cover in the surrounding landscape favored species richness. Additionally, species composition differed significantly between agroforests and forests, suggesting that while these systems can sustain part of the biodiversity, they cannot fully substitute native forests.

In Chapter 2, by directly assessing amphibian and reptile diversity in 30 cocoa agroforests, we found that the richness and diversity of these groups were largely determined by landscape-scale variables. For amphibians, pasture cover favored taxonomic and phylogenetic diversity, whereas edge density and landscape fragmentation had negative effects on functional diversity. For reptiles, forest cover and edge density were key factors for species richness and phylogenetic diversity, while local variables such as temperature and humidity influenced functional diversity. These results highlight that biodiversity conservation in agroforests depends not only on their local characteristics but also on the broader landscape context in which they are embedded.

Finally, Chapter 3 examined multidimensional beta diversity in shaded cocoa agroforests across three regions with contrasting land-use contexts. For amphibians, the highest values of taxonomic and phylogenetic beta diversity were found in the high forest cover (HFC) and low forest cover (LFC) regions, while for reptiles, beta diversity peaked in the HFC region. In the high agroforest cover region (HAC), both amphibians and reptiles exhibited the lowest beta diversity across all dimensions, suggesting biotic homogenization. Environmental and spatial predictors influenced beta diversity differently depending on the taxonomic group, region, and diversity dimension. For amphibians, differences in shade tree abundance and pasture cover were key predictors in HFC, while in LFC, geographic distance played a dominant role, consistent with dispersal limitation. In HAC, vegetation structure failed to promote differentiation, contributing to community homogenization. For reptiles, beta diversity in HAC was associated with variation in canopy cover, while in HFC, forest cover and spatial distance influenced phylogenetic differentiation. In LFC, geographic distance increased phylogenetic beta diversity, while greater differences in grass cover reduced it, highlighting contrasting mechanisms of lineage differentiation and homogenization across spatial scales. These findings underscore the importance of adopting context-specific conservation strategies that consider both spatial configuration and environmental heterogeneity to preserve taxonomic, functional, and evolutionary diversity in tropical human-modified landscapes.

The findings of this thesis have important implications for the conservation of herpetofaunal diversity in agroforests landscapes. First, they reinforce the idea that shaded agroforest systems can serve as complementary habitats for many species, particularly reptiles, especially when they are located in landscapes with greater forest cover and complex vegetation structures. However, since species composition in agroforests differs from that in native forests, these systems cannot replace the conservation of primary forest areas. Therefore, management strategies that maintain structural heterogeneity within agroforests systems and reduce landscape fragmentation could enhance their capacity to support diverse communities.

Additionally, the results suggest that conservation policies in cocoa-dominated landscapes should adopt a multi-scale approach, integrating actions that promote connectivity between agroforests and forest fragments. The implementation of ecological corridors, the conservation of shade trees, and the restoration of degraded areas could help mitigate the negative effects of deforestation on these two taxonomic groups. Furthermore, given that amphibian and reptile responses to landscape structure vary among species and biodiversity dimensions, it is crucial to design differentiated management strategies that consider the specific ecological needs of each taxon.

In conclusion, this thesis provides key evidence on the role of shaded agroforests systems in the conservation of herpetofauna in the Atlantic Forest. While these systems can contribute to biodiversity persistence in agricultural landscapes, their effectiveness depends on landscape-scale factors and local management. Therefore, integrating agroforests into conservation strategies should be based on multidimensional approaches that consider taxonomic, functional, and phylogenetic diversity, ensuring that these systems continue to provide refuge for amphibian and reptile species in the long term.

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Appendixes

Appendix A. Predation of the Black-Spotted Casque-Headed Treefrog, *Trachycephalus nigromaculatus* (Tschudi, 1838), by the Ocellated Treefrog, *Itapotihyla langsdorffii* (Duméril and Bibron, 1841), in a cacao agroforestry system in southern Bahia, Brazil

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Main text

Predation of the Black-Spotted Casque-Headed Treefrog, *Trachycephalus nigromaculatus* (Tschudi, 1838), by the Ocellated Treefrog, *Itapotihyla langsdorffii* (Duméril and Bibron, 1841), in a cacao agroforestry system in southern Bahia, Brazil

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Predation is a fundamental ecological interaction wherein one organism (predator), hunts and consumes another organism (prey), to obtain the energy required for survival (Minelli, 2008). The ecological role of predators in ecosystems is important because they can influence and control the distribution, abundance, and diversity of their prey (Molles and Sher, 2019). Additionally, predators can facilitate the coexistence of several species in diverse habitats (Melguizo-Ruiz et al., 2020). For instance, amphibian predators occupy essential positions within the food chain and feed on a wide variety of invertebrates and small vertebrates, including intra and inter-specific predation of anurans (Solé and Rödder, 2010). Therefore, amphibians can effectively regulate the populations of their prey (Cortés-Gomez et al., 2015), which is essential for the stability of the ecosystem.

The Ocellated Treefrog, *Itapotihyla langsdorffii* (Duméril and Bibron, 1841), is a large-sized anuran (mean snout-vent length 103 mm in females; 81 mm in males; Vrcibradic et al., 2009), belonging to the family Hylidae (Frost, 2023). This species is found in the Atlantic Forest of Brazil, between Bahia and Rio Grande do Sul states, as well as in northeastern Argentina and Paraguay (Arzabe and Loebmann, 2006; Lingnau et al., 2006; Cazelli and Moura, 2012; Frost, 2023; Airaldi-Wood et al., 2021). *I. langsdorffii* can be found in the treetops and shrubs of tropical rainforests in pristine habitats, and breeds in both temporary and permanent pools within the forest (Arzabe and Loebmann, 2006). However, the species can also be observed in human-altered habitats such as cocoa agroforestry systems (Teixeira et al., 2015).

The Black-spotted Casque-headed Treefrog, *Trachycephalus nigromaculatus* (Tschudi, 1838), belonging to the family Hylidae, is also a large-sized tree frog with a snout-vent length of females ranging from 80 to 92 mm, while males measure around 70 to 80 mm (Haddad et al., 2013). Its distribution covers the coastal regions of southern Brazil, extending from the southeast (Atlantic Forest biome) and the central-west (Cerrado biome) region of the country (Dias et al., 2010; Martins and Assalim, 2019; Frost, 2023). This frog is usually found inside bromeliads in primary and secondary forests and in coastal "restinga" scrub (IUCN SSC, 2023), as well as in cocoa agroforestry systems (Teixeira et al., 2015) and urban areas (Silveira, 2006). While specific evidence on the prey of *T. nigromaculatus* is lacking, other species within the same genus have been recorded primarily consuming a variety of invertebrates and small vertebrates, such as lizards in *T. typhonius* (Marín and Mora, 2022), bats in *T. "vermiculatus"* (Strüssmann and Sazima, 1991), and other frog species (Dundee and Liner, 1985; Loebmann, 2013), including conspecifics individuals (Parmelee, 1999).

Figure 1. An adult Ocellated Treefrog, Itapotihyla langsdorffii (snout-vent length = 117 mm) feeding on an adult Black-spotted Casque-headed Treefrog, Trachycephalus nigromaculatus in a cocoa agroforestry system located in the municipality of Belmonte, Bahia state, Brazil. Photos by M.J. Cervantes-López (left) and G. Alves-Ferreira (right).

Figure 2. An adult Black-spotted Casque-headed Treefrog, *Trachycephalus nigromaculatus* (approx. snout-vent length = 70-80 mm) registered in a cacao agroforestry system from the municipality of Belmonte, Bahía, Brazil. Photo by M.J. Cervantes-López.

On 9 March 2023, at 12:23 h, during fieldwork for the network project "Eco-nomia das Cabrucas", we recorded an adult individual of *I. langsdorffii* (117 mm snout-vent length) with a specimen of *T. nigromaculatus* in its mouth (Fig. 1). This predatory event was observed in a cocoa agroforestry system situated in the municipality of Belmonte, state of Bahia, Brazil (15.8780°S, 39.3684°W, 67 m elevation). We found both amphibians positioned on a tree trunk (approximately 1.70 m in height), with the prey (*T. nigromaculatus*) already halfway inside the mouth of the predator (*I. langsdorffii*) (Fig. 1). The prey was being consumed starting from the head, exhibiting complete immobilization with no attempts to escape. We did not observe any toxic secretion being released by *I. langisdorfii* during the predation event. *T. nigromaculatus* can be identified by the presence of small reddish spots on the back (Fig. 2), an unmistakable feature that proves to be one of the most important visual characteristics for recognising this anuran (Martins and Assalim, 2019).

Although species of the genus *Trachycephalus* employ toxic secretions from their skin glands as a defence mechanism against predators, predation of this species appears to be a common occurrence in nature, including by other frogs (Yeager et al., 2019). Previous studies have documented other *Trachycephalus* species being preyed upon by the frogs *Chacophrys pierottii* (Villafañe et al., 2017), *Ceratophrys aurita* (Solé et al., 2010), and by *Leptodactylus* cf. *latrans* (Mira-Mendes et al., 2012). Furthermore, *Trachycephalus* species have been preyed upon by several other animals, including insects (Hernández-Baltazar et al., 2020), snakes (Solé et al., 2010; García et al., 2020; Roberto and Souza, 2020; Dias-Silva et al., 2021; Hernández-Sánchez and Guevara-Alvarado, 2022), birds (Nuñez and Pérez, 2021), and primates (Garbino et al., 2020). However, there is evidence that *I. langsdorffii* can prey on other amphibian species, such as *Physalaemus crombiei*, *Scinax argyreornatus* (Vrcibradic et al., 2009), and juveniles of *Nyctimantis arapapa* (Sales-de-Aquino et al. 2012). Here, we report the first record of *I. langsdorffii* feeding on a hylid with toxic skin of the genus *Trachycephalus*. This record increases knowledge about the natural history of anurans that inhabit the Brazilian Atlantic Forest, by highlighting the ecological relationship between two species of anurans. Furthermore, this atypical case of predation between *I. langsdorffii* and *T. nigromaculatus* may open new avenues of research on the possible immunity of *I. langsdorffii* to toxins present in other amphibian species. Indeed, this could have implications for understanding the dynamics of coevolution between predator and prey, as well as to facilitate comprehension on the mechanisms that contribute to potential toxin resistance.

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Appendix B. Photographs of some amphibian and reptile species observed within shaded cocoa agroforests in southeastern Bahia, Brazil

Allophryne relicta

Allobates olfersioides

Rhinella crucifer

Rhinella hoogmoedi

Vitreorana baliomma

Haddadus binotatus

Thoropa miliaris

Gastrotheca recava

Aplastodiscus ibirapitanga

Boana albomarginata

Boana atlantica

Boana faber

Boana pombali

Dendropsophus haddadi

Hylomantis granulosa

Itapotihyla langsdorffii

Nyctimantis brunoi

Ololygon strigilata

Phyllodytes magnus

Phyllomedusa bahiana

Pithecopus nordestinus

Trachycephalus mesophaeus

Adenomera thomei

Leptodactylus mystaceus

Scinax juncae

Chiasmocleis sp.

Physalaemus camacan

Proceratophrys renalis

Stereocyclops incrassatus

Macrogenioglottus alipioi

Bahius bilineatus

Pristimantis paulodutrai

Siphonops annulatus

Corallus hortulanus

Dipsas catesbyi

Oxybelis aeneus

Atractus guentheri

Drymarchon corais

Dipsas indica

Imantodes cenchoa

Oxyrhopus guibei

Siphlophis compressus

Xenopholis scalaris

Micrurus corallinus

Bothrops leucurus

Anolis punctatus

Gymnodactylus darwinii

Leposoma scincoides

Enyalius catenatus

Polychrus marmoratus

Phyllopezus lutzae

Coleodactylus meridionalis

Tropidurus torquatus

Kentropyx calcarata