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**Dinâmica e Diversidade de Squamata na Amazônia Brasileira: Impactos dos
Gradientes Ambientais, Tendências Temporais e Métodos Amostrais**

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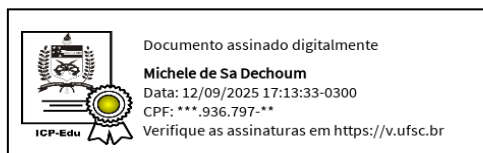
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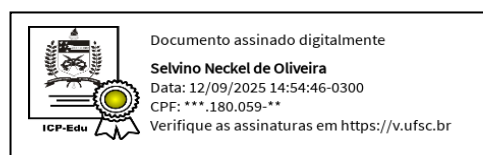
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Coordenação do Programa de Pós-Graduação



Prof.(a) Selvino Neckel de Oliveira
Orientador(a)

Florianópolis, 2025.

Para a Amazônia e todos os seres vivos que nela habitam.

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“O índio chorou
O branco chorou
Todo mundo está chorando
A amazônia está queimando
Ai, ai, que dor
Ai, ai, que horror”
(Lamento da Raça - Boi Garantido)

“Nenhum outro planeta no sistema solar é uma boa casa para os seres humanos; temos esse mundo ou nada. Essa é uma percepção muito poderosa.”
(Sagan, Carl)

RESUMO

Esta tese investiga os determinantes da organização de comunidades de Squamata (lagartos e serpentes) na Amazônia Brasileira, adotando uma abordagem integrada que abrange a influência de gradientes ambientais, dinâmicas temporais e efeitos dos métodos de amostragem sobre a diversidade taxonômica e funcional. O estudo é constituído de três artigos inter-relacionados que exploram, de maneira complementar, os aspectos ecológicos e metodológicos que moldam a estrutura dessas comunidades, oferecendo subsídios para estratégias de conservação em um dos ecossistemas mais complexos e ameaçados do planeta.

No primeiro artigo, “Temporal Patterns in Lizard and Snake Communities: Contrasting Responses to Environmental Factors in Carajás National Forest, Pará, Brazil”, foram investigadas respostas temporais de comunidades de Squamata a variáveis ambientais como a densidade de vegetação e elevação, a partir de levantamentos padronizados realizados de 2015 a 2022 na Floresta Nacional de Carajás. Os resultados indicam que as assembléias de lagartos respondem à cobertura vegetal e às variações topográficas, mostrando maiores abundâncias e riqueza em áreas com vegetação densa. Em contraste, as serpentes apresentaram respostas mais sutis, com a elevação emergindo como o principal preditor de sua distribuição. Destaca-se também uma tendência de queda na abundância de lagartos após 2019, sugerindo impactos ambientais ou mudanças nos padrões de atividade.

No segundo artigo, “Environmental influence on the composition of Squamata assemblages in the Brazilian Amazon”, os efeitos de variáveis climáticas, estrutura da vegetação, nutrientes do solo e proximidade à água foram avaliados em 13 locais de florestas de terra firme. Os resultados mostram que, para lagartos, áreas próximas à água, com solo fértil, dossel elevado e temperaturas máximas mais altas, apresentam maiores abundâncias e a sazonalidade da temperatura impulsiona a riqueza de espécies. Já para as serpentes, altos níveis de precipitação durante o período úmido estão associados a menores abundâncias, sem efeitos significativos sobre a composição taxonômica, evidenciando desafios na amostragem deste grupo.

No terceiro artigo, “Sampling method effects on taxonomic and functional diversity patterns of lizards and snakes in the Brazilian Amazon”, são comparados três métodos – armadilhas de interceptação e queda, busca ativa e encontros ocasionais – para estimar a diversidade taxonômica e funcional. Para lagartos, as armadilhas pitfall se mostraram mais eficazes, registrando 45 espécies e maior número de indivíduos, enquanto para serpentes os encontros ocasionais foram mais produtivos, com 43 espécies detectadas. Embora os métodos influenciem significativamente as estimativas de diversidade taxonômica e a composição das comunidades, não há

diferenças significativas nas medidas de diversidade funcional entre os métodos, indicando que, apesar das discrepâncias na detecção de espécies, os traços ecológicos abrangidos permanecem semelhantes em toda a comunidade.

Em síntese, os três estudos demonstram que os gradientes ambientais e a variação temporal exercem papel crucial na formação das assembleias de Squamata na Amazônia, e que a escolha dos métodos de amostragem afeta fortemente os inventários taxonômicos, mas não altera de maneira significativa a avaliação da diversidade funcional. Esses achados ressaltam a necessidade de abordagens integradas e multi-metodológicas para obter inventários completos e para orientar estratégias de conservação em ecossistemas tropicais.

Palavras-chave: Squamata, Amazônia, diversidade taxonômica, diversidade funcional, gradientes ambientais, métodos de amostragem, dinâmicas temporais.

ABSTRACT

This thesis investigates the determinants of community organization in Squamata (lizards and snakes) in the Brazilian Amazon, adopting an integrated approach that encompasses the influence of environmental gradients, temporal dynamics, and the effects of sampling methods on taxonomic and functional diversity. The study is composed of three interrelated articles that complementarily explore the ecological and methodological aspects shaping the structure of these communities, providing support for conservation strategies in one of the most complex and threatened ecosystems on the planet.

In the first article, “Temporal Patterns in Lizard and Snake Communities: Contrasting Responses to Environmental Factors in Carajás National Forest, Pará, Brazil,” temporal responses of Squamata communities to environmental variables such as vegetation density and elevation were investigated from standardized surveys conducted between 2015 and 2022 in Carajás National Forest. The results indicate that lizard assemblages respond to vegetation cover and topographic variations, displaying higher abundances and richness in areas with dense vegetation. In contrast, snakes exhibited more subtle responses, with elevation emerging as the primary predictor of their distribution. There is also a noted trend of decreasing lizard abundance after 2019, suggesting environmental impacts or changes in activity patterns.

In the second article, “Environmental influence on the composition of Squamata assemblages in the Brazilian Amazon,” the effects of climatic variables, vegetation structure, soil nutrients, and proximity to water were evaluated in 13 sites within terra firme forests. The results show that, for lizards, areas near water, with fertile soil, elevated canopy, and higher maximum temperatures, exhibit greater abundances and that temperature seasonality drives species richness. For snakes, high levels of precipitation during the wet season are associated with lower abundances, with no significant effect on taxonomic composition, highlighting the challenges of sampling this group.

In the third article, “Sampling method effects on taxonomic and functional diversity patterns of lizards and snakes in the Brazilian Amazon,” three methods—pitfall traps with drift fences, active search, and occasional encounters—are compared to estimate taxonomic and functional diversity. For lizards, pitfall traps proved to be the most effective, recording 45 species and a higher number of individuals, while for snakes occasional encounters were more productive, with 43 species detected. Although the methods significantly influence taxonomic diversity estimates and community composition, there are no significant differences in measures of functional diversity among methods, indicating that despite discrepancies in species detection, the ecological traits encompassed remain similar throughout the community.

In summary, the three studies demonstrate that environmental gradients and temporal variation play a crucial role in shaping Squamata assemblages in the Amazon, and that the choice of sampling methods strongly affects taxonomic inventories without significantly altering the assessment of functional diversity. These findings emphasize the need for integrated and multi-method approaches to obtain complete inventories and guide conservation strategies in tropical ecosystems.

Keywords: Squamata, Amazon, taxonomic diversity, functional diversity, environmental gradients, sampling methods, temporal dynamics.

RESUMO EXPANDIDO

Introdução

A compreensão dos fatores que determinam a distribuição da biodiversidade no tempo e espaço constitui uma das questões centrais em ecologia, com implicações diretas para a conservação de ecossistemas tropicais. Na Amazônia brasileira, o maior bioma de floresta tropical úmida do planeta com aproximadamente seis milhões de km², essa questão torna-se particularmente relevante devido à excepcional diversidade biológica e às crescentes pressões antrópicas sobre os ecossistemas naturais. A distribuição das espécies neste bioma reflete a interação complexa entre processos determinísticos, como gradientes ambientais e eventos históricos, e processos estocásticos, que operam em escalas mais localizadas. Entre os vertebrados, os répteis Squamata (lagartos e serpentes) representam modelos particularmente adequados para investigações ecológicas devido à sua natureza ectotérmica, que resulta em estreita dependência das condições ambientais, mobilidade limitada e associação específica com microhabitats. Atualmente, são reconhecidas aproximadamente 425 espécies de Squamata para a Amazônia brasileira, número que continua aumentando através de novas descrições taxonômicas e registros geográficos. Entretanto, o conhecimento sobre a distribuição e ecologia desses grupos permanece desigual pela região, com diversas áreas subamostradas ou completamente inexploradas. Este cenário é agravado pelos desafios metodológicos inerentes ao estudo desses animais, particularmente as serpentes, que apresentam baixa detectabilidade em campo. Diferentes métodos de amostragem podem produzir resultados contrastantes na detecção de espécies, influenciando não apenas as estimativas de diversidade taxonômica, mas também a compreensão dos padrões de diversidade funcional nas comunidades. Diante desse contexto, torna-se fundamental investigar como gradientes ambientais, dinâmicas temporais e métodos de amostragem influenciam a estrutura das comunidades de Squamata, integrando análises em múltiplas escalas espaciais e temporais para fornecer subsídios robustos para estratégias de conservação na Amazônia.

Objetivos

Esta tese teve como objetivo geral investigar o papel dos gradientes ambientais, dinâmica temporal e métodos de amostragem na estruturação da diversidade taxonômica e funcional de assembleias de lagartos e serpentes na Amazônia brasileira. Para alcançar esse objetivo, a pesquisa foi estruturada em três capítulos com objetivos específicos complementares. No Capítulo 1, objetivamos: (1) analisar a influência de variáveis ambientais incluindo vegetação, elevação do terreno, temperatura e umidade na composição, abundância e riqueza das assembleias de lagartos e serpentes na Floresta Nacional de Carajás; (2) examinar as tendências temporais dos parâmetros comunitários (riqueza e abundância) de lagartos e serpentes, considerando variações no esforço de amostragem no período de 2015 a 2023; e (3) compreender as relações entre os gradientes ambientais e a dinâmica das comunidades, evidenciando implicações ecológicas relevantes para a conservação do ecossistema estudado. No Capítulo 2, buscamos: (1) identificar quais variáveis ambientais, estruturais e climáticas, influenciam significativamente a riqueza de espécies de lagartos e serpentes em 13 áreas de floresta no bioma

Amazônico; (2) determinar como essas variáveis ambientais afetam a abundância de lagartos e serpentes nas áreas amostradas; e (3) avaliar como a estrutura ambiental e o clima moldam a composição das comunidades de lagartos e serpentes em diferentes regiões da Amazônia brasileira. No Capítulo 3, propusemos: (1) comparar a eficácia de três métodos de amostragem – armadilhas de interceptação e queda (Pitfall traps), busca ativa e encontros ocasionais – na obtenção de estimativas de diversidade de lagartos e serpentes; (2) determinar como a escolha dos métodos de amostragem influencia as estimativas de diversidade utilizando números de Hill para riqueza, espécies comuns e dominantes; e (3) testar se as diferentes técnicas de amostragem afetam as medidas de diversidade funcional, avaliando se a gama de traços ecológicos dos répteis permanece consistente apesar das discrepâncias na detecção das diferentes espécies.

Metodologia

A pesquisa foi desenvolvida utilizando uma abordagem integrada em múltiplas escalas espaciais e temporais na Amazônia brasileira. No Capítulo 1, os dados foram coletados em 68 parcelas distribuídas na Floresta Nacional de Carajás, Pará, seguindo o protocolo RAPELD (Rapid Assessment and Permanent Ecological Longitudinal Plots). O monitoramento foi realizado entre 2015 e 2023, com 26 parcelas em ambientes ripários amostradas durante todo o período, 29 parcelas em floresta amostradas por cinco anos e 13 parcelas em canga amostradas por dois anos. Cada parcela consistiu em um transecto de 250 metros posicionado ao longo das curvas de nível do terreno para minimizar a heterogeneidade ambiental. As amostragens incluíram buscas visuais diurnas (15:30-18:00h) e noturnas (19:00-21:00h) realizadas por dois herpetólogos especializados, totalizando quatro horas/pessoa de esforço por parcela. Foram coletadas variáveis ambientais incluindo NDVI (Normalized Difference Vegetation Index), elevação, temperatura e umidade. As análises estatísticas incluíram modelos lineares generalizados (GLM) com distribuição binomial negativa para abundância e Poisson para riqueza, além de análise de redundância (RDA) para composição das comunidades. No Capítulo 2, expandimos a investigação para 13 localidades distribuídas em diferentes regiões biogeográficas da Amazônia brasileira, com amostragens realizadas entre 2019 e 2023 durante o período seco (maio a dezembro). Em cada localidade, estabelecemos três transectos de 1 km com armadilhas de interceptação e queda em configuração Y instaladas a 0, 500 e 1.000 metros, operando por nove noites consecutivas (total de 1.053 armadilhas-noite). Buscas visuais padronizadas foram conduzidas em seções de 250 metros de cada transecto, com esforço total de 234 pessoas-hora. Coletamos inicialmente 19 variáveis bioclimáticas e estruturais, restando 10 após análise de colinearidade. As análises incluíram GLMs, PERMANOVA e RDA. No Capítulo 3, utilizamos os dados das mesmas 13 localidades para comparar sistematicamente a eficácia dos três métodos de amostragem. Para análises de diversidade funcional, compilamos dados de traços ecológicos incluindo tamanho corporal, uso de habitat, dieta, período de atividade e modo reprodutivo. Utilizamos números de Hill ($q = 0, 1, 2$) para quantificar diversidade taxonômica e funcional, além de análises de composição via PCoA e modelos lineares generalizados mistos (GLMM) para testar diferenças entre métodos.

Resultados e Discussão

Os resultados revelaram padrões complexos e complementares na estruturação das comunidades de Squamata amazônicas. No Capítulo 1, registramos 56 espécies (16 lagartos e 40 serpentes) na Floresta Nacional de Carajás. As comunidades de lagartos demonstraram forte resposta aos gradientes ambientais, com o NDVI explicando 41,7% da variação comunitária (R^2 ajustado = 0,401) e influenciando significativamente tanto a abundância ($\beta = 0,391$, $p = 0,002$) quanto a riqueza de espécies ($\beta = 0,257$, $p = 0,015$). A elevação mostrou efeito negativo sobre a riqueza de lagartos ($\beta = -0,204$, $p = 0,020$) e foi o principal preditor para serpentes, afetando negativamente tanto abundância ($\beta = -0,502$, $p < 0,001$) quanto riqueza ($\beta = -0,442$, $p < 0,001$). As análises temporais revelaram tendências contrastantes entre habitats: em ambientes florestais, a abundância de lagartos apresentou tendência positiva (0,2236 por ano) enquanto a riqueza tendeu a declinar (-0,0302 por ano), sugerindo dominância crescente de poucas espécies, particularmente *Chatogekko amazonicus* que representou 94% das capturas. Em ambientes ripários, observamos padrão inverso, com declínio na abundância de lagartos (-0,0265 por ano) mas aumento sutil na riqueza (0,0160 por ano). As serpentes mostraram maior estabilidade temporal, embora com baixas taxas de detecção.

No Capítulo 2, analisando 13 áreas distribuídas pela Amazônia, registramos 1.169 indivíduos pertencentes a 109 espécies (55 lagartos e 56 serpentes). A abundância de lagartos foi positivamente associada à proximidade de corpos d'água (HAND), maiores concentrações de nutrientes no solo, altura do dossel e temperatura máxima do mês mais quente. A riqueza de lagartos respondeu principalmente à sazonalidade térmica. Para serpentes, apenas a precipitação do mês mais úmido mostrou efeito significativo, reduzindo a abundância. A composição das comunidades de lagartos foi significativamente influenciada por múltiplos fatores: sazonalidade térmica ($F = 2,429$, $p = 0,006$), precipitação do mês mais úmido ($F = 2,329$, $p = 0,009$), precipitação do trimestre mais frio ($F = 2,313$, $p = 0,016$) e densidade de árvores ($F = 1,829$, $p = 0,049$). As comunidades de serpentes não mostraram associações significativas com as variáveis ambientais testadas, possivelmente devido às limitações de detecção e tamanho amostral reduzido (160 indivíduos em 13 localidades).

O Capítulo 3 revelou eficácias marcadamente distintas entre métodos de amostragem. Para lagartos, as armadilhas pitfall foram mais efetivas, capturando 45 espécies (578 indivíduos), seguidas por busca ativa (33 espécies, 319 indivíduos) e encontros ocasionais (30 espécies, 92 indivíduos). Para serpentes, o padrão se inverteu completamente: encontros ocasionais registraram 43 espécies (79 indivíduos), busca ativa 23 espécies (40 indivíduos) e pitfall apenas 11 espécies (14 indivíduos). A diversidade taxonômica diferiu significativamente entre métodos para ambos os grupos ($p < 0,001$ para todos os números de Hill). Surpreendentemente, a diversidade funcional não apresentou diferenças significativas entre métodos ($p > 0,32$ para todos os valores de q), sugerindo que, apesar dos vieses taxonômicos, todos os métodos capturam amplitudes similares de traços funcionais. Este padrão pode indicar redundância funcional nas comunidades tropicais ou limitações na sensibilidade das métricas categóricas utilizadas.

A integração desses resultados revela que lagartos e serpentes respondem

diferentemente aos gradientes ambientais amazônicos. A forte associação dos lagartos com a estrutura da vegetação reflete a importância de microhabitats térmicos e disponibilidade de refúgios, enquanto a influência da elevação sugere que a heterogeneidade topográfica contribui para manutenção da diversidade através de gradientes ambientais. O padrão observado em Carajás, onde elevações mais altas com vegetação de canga abrigam espécies heliófilas especializadas como *Tropidurus oreadicus*, enquanto elevações baixas com floresta densa suportam comunidades mais ricas, exemplifica como gradientes elevacionais criam assembleias distintas em distâncias relativamente curtas.

Considerações Finais

Esta tese demonstra que gradientes ambientais e variações temporais exercem papel fundamental na estruturação das assembleias de Squamata na Amazônia brasileira, com respostas distintas entre lagartos e serpentes. A vegetação emerge como principal driver para comunidades de lagartos, enquanto serpentes respondem mais fortemente a gradientes topográficos. A heterogeneidade ambiental, manifestada através de mosaicos de habitats com diferentes estruturas vegetacionais, regimes hídricos e características edáficas, é crucial para manutenção da excepcional diversidade de répteis amazônicos. Os padrões temporais observados, embora sutis, sugerem mudanças em curso que demandam monitoramento contínuo, especialmente considerando as crescentes pressões antrópicas sobre estes ecossistemas. A escolha do método de amostragem influencia dramaticamente os inventários taxonômicos, com pitfall traps sendo mais eficazes para lagartos e encontros ocasionais para serpentes, evidenciando a necessidade de abordagens multi-metodológicas para caracterização completa das comunidades. A aparente estabilidade da diversidade funcional entre métodos sugere redundância ecológica, mas também aponta para a necessidade de refinamento nas métricas funcionais utilizadas. Estes achados fornecem subsídios importantes para estratégias de conservação, indicando que a preservação da heterogeneidade ambiental em múltiplas escalas espaciais é essencial para manter a diversidade de Squamata. Recomendamos que futuros programas de monitoramento e conservação considerem as respostas táxon-específicas aos gradientes ambientais, empreguem múltiplos métodos de amostragem e incorporem análises funcionais mais refinadas para compreender plenamente os mecanismos que mantêm a biodiversidade em ecossistemas tropicais megadiversos.

Palavras-chave: Squamata; Gradientes ambientais; Diversidade funcional; Amazônia; Métodos de amostragem.

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1. INTRODUÇÃO GERAL

Uma das questões mais intrigantes em ecologia refere-se aos determinantes da distribuição da biodiversidade no tempo e no espaço. A distribuição das espécies pode refletir a interação entre processos estocásticos e determinísticos, e compreender esses processos é essencial para elucidar a história evolutiva das comunidades atuais. (Elith & Leathwick, 2009). Estudos neste tema têm se tornado particularmente relevantes diante da grande quantidade de intervenções humanas nos ecossistemas naturais, incluindo perda, degradação e fragmentação de habitats pelo uso da terra e, conseqüentemente, declínio expressivo da biodiversidade em escala global (Pereira et al., 2010; Rands et al., 2010; Haddad et al., 2015).

Processos determinísticos incluem fatores ambientais e históricos que operam em escalas maiores, como as mudanças climáticas ocorridas durante o Pleistoceno, que teriam influenciado a configuração atual da biogeografia das espécies na Amazônia, ou o soerguimento dos Andes, que reverteram o fluxo de rios amazônicos, alteraram os regimes de chuva e o clima regional, criando novos habitats e permitindo eventos de especiação (Hoorn, 2010, Chase & Myers, 2012). Em contrapartida, eventos estocásticos, como furacões ou outras perturbações aleatórias, tendem a ter efeitos mais localizados, promovendo alterações drásticas nas comunidades, como pode ter ocorrido com populações de lagartos na América Central (Donihue, 2020). Essa distinção ressalta que, enquanto os processos determinísticos impõem padrões regionais, os eventos estocásticos são responsáveis por diversificar a composição local das comunidades.

O bioma Amazônia contém a maior e mais diversa floresta tropical úmida do planeta, inserida em nove países da América do Sul e com uma área aproximada de seis milhões de km² (Haseyama & Carvalho, 2011). Somente no Brasil, o bioma ocupa cerca de 40% do território e exerce serviços ambientais essenciais, tais como a regulação do clima, armazenamento de carbono e desempenho do regime hidrológico (Nobre, 2002; Fearnside, 2006). A região Amazônica apresenta uma alta complexidade estrutural, sendo um amplo mosaico de formações, com grande heterogeneidade ambiental, sendo determinante para a grande biodiversidade encontrada neste bioma independentemente da escala geográfica (Hoorn et al., 2010).

A alta diversidade biológica na Amazônia tem sido objeto de estudos por parte de pesquisadores de todo o mundo, e diversas hipóteses surgiram acerca dos fatores responsáveis por sua origem e manutenção e têm sido testadas, tais como a atuação de barreiras geográficas à dispersão, flutuações climáticas e mudanças geomorfológicas históricas (Wallace, 1852; Haffer, 1969; Cracraft, 1985; Bush, 1994; Racheli & Racheli, 2004; Wüster et al., 2005; Antonelli et al., 2009; Hoorn et al., 2010; Leite & Rogers, 2013). Trabalhos envolvendo diferentes táxons, como plantas (Dexter et al., 2012), borboletas (Racheli & Racheli, 2004), anfíbios (Dias-Terceiro et al., 2015, Simões, et al., 2008), aves (Heyes et al., 2004; Ribas et al., 2012; Pomara et al., 2014, Fernandes et al., 2013), e mamíferos (Ayres, et al., 1992; Boubli, et al., 2015; Patton, et al., 1994) descrevem o papel dos grandes rios amazônicos como barreira à dispersão, fazendo com que as regiões de interflúvio sejam configuradas como áreas de pronunciado endemismo de espécies e de linhagens intraespecíficas.

Outro mecanismo que também tem sido apontado para a regionalização da biodiversidade é a hipótese dos gradientes ambientais. Diferentemente do isolamento alopátrico, que enfatiza barreiras físicas à dispersão, essa hipótese propõe que a diferenciação contínua de populações ocorra gradualmente ao longo de clinas ambientais, impulsionada pela variabilidade dos habitats e pelos processos adaptativos (Endler, 1977; Leite & Rogers, 2013). Diversos estudos têm evidenciado essa dinâmica em diferentes grupos taxonômicos, como roedores (Patton & Smith, 1992), aves (Dingle et al., 2006) e anfíbios (Funk et al., 2007), demonstrando que a variação ambiental pode fomentar a divergência mesmo na presença de fluxo gênico. Dessa forma, integrar os mecanismos relacionados tanto a barreiras geográficas quanto a gradientes ecológicos é fundamental para compreender a complexa história evolutiva e a excepcional diversidade biológica da Amazônia (Antonelli et al., 2010; Smith et al., 2014).

A ordem Squamata, que engloba lagartos, serpentes e anfisbenas, é o clado mais diverso de répteis, com 811 espécies reconhecidas para o Brasil (Guedes et al., 2023). O norte do Brasil concentra quase metade dessa diversidade, com 425 espécies registradas até o momento (Guedes et al., 2023). Além disso, a riqueza de escamados tem aumentado continuamente, impulsionada pela descrição de novas espécies – seguindo Uetz (2010), foram descritas aproximadamente 1.000 novas espécies de répteis a cada duas décadas, com um acréscimo expressivo somente

nos últimos 20 anos – e pelo incremento da distribuição de muitas outras espécies por meio de novos registros geográficos (Moura & Jetz, 2021).

Entretanto, devido à dificuldade de acesso a diferentes partes da região amazônica, o conhecimento acerca da diversidade deste grupo é desigual pela região, com diversos locais com poucas amostragens ou às vezes inexplorados (Avila-Pires et al., 2009; Guedes et al., 2018; Frazão et al., 2020). Um desafio adicional é que diferentes métodos de amostragem podem produzir resultados contrastantes na detecção de espécies. Estudos recentes sugerem que enquanto armadilhas de interceptação e queda são mais eficientes para lagartos, encontros ocasionais e busca ativa são mais efetivos para serpentes (Ribeiro-Júnior et al., 2008; Fraga et al., 2014). Esta variação metodológica pode afetar não apenas as estimativas de diversidade taxonômica, mas também nossa compreensão dos padrões de diversidade funcional nas comunidades, visto que são índices calculados a partir das espécies efetivamente detectadas e seus atributos (eg. morfologia, dieta, atividade).

Lagartos constituem modelos bastante apropriados em investigações ecológicas, pois são localmente abundantes, relativamente fáceis de coletar e a ocorrência das espécies tende a ser associada aos diferentes microhabitats que suprem seus diferentes requerimentos, considerando-se que a maior parte deste grupo possui um pequeno tamanho relativo, mobilidade limitada e baixa demanda de energia e água (Garda et al., 2013). Sendo assim, são bons bioindicadores para investigar o efeito do ambiente sobre organismos em diferentes escalas (Werneck & Colli, 2006; Werneck et al., 2009; Camargo et al., 2010). Atualmente, são reconhecidas cerca de 165 espécies de lagartos para a região amazônica (Censo da Biodiversidade/Museu Goeldi, 2022), com tendência de aumento devido a novas descrições e revisões taxonômicas (D'angiolella et al., 2011; Peloso et al., 2011; Murphy e Jowers, 2013).

As serpentes, embora representem o grupo mais rico entre os Squamata do Brasil, apresentam desafios únicos para estudos ecológicos devido à sua baixa detectabilidade em campo (Fraga et al., 2014). Ocupando diversos microhabitats, incluindo ambientes aquáticos, terrestres, arborícolas e fossoriais (Fraga et al., 2013), as serpentes requerem abordagens metodológicas específicas e períodos mais longos de amostragem para uma adequada caracterização de suas comunidades. Atualmente são conhecidas cerca de 235 espécies de serpentes para

a Amazônia brasileira (Costa et al., 2021), número que tende a aumentar com novos estudos e amostragens em áreas pouco exploradas.

A estrutura das comunidades de Squamata pode ser influenciada por diversos fatores ambientais. Em escala local, variáveis como a cobertura vegetal, elevação, temperatura e umidade podem afetar significativamente tanto a abundância quanto a composição de espécies. Por exemplo, comunidades de lagartos e serpentes frequentemente mostram forte resposta à estrutura da vegetação (Vitt et al. 2008; Peixoto et al. 2022), gradientes de elevação, e distância para o corpo d'água (Fraga et al., 2011, Faria et al., 2019). Além disso, variações temporais nessas comunidades podem revelar padrões importantes de dinâmica populacional e respostas às mudanças ambientais ao longo do tempo.

Monitoramentos de longo prazo, como o proposto pelo método RAPELD (Rapid Assessment + Projeto Ecológico de Longa Duração) (Magnusson et al., 2005), constituem uma alternativa fundamental para preencher as lacunas de conhecimento sobre estes grupos. Tais metodologias permitem não apenas aumentar a taxa de detecção de espécies, especialmente para grupos mais crípticos como as serpentes, mas também compreender padrões temporais de variação nas comunidades e suas respostas a mudanças ambientais, através de um método padronizado, modular e escalonável de coleta de dados.

Considerando a grande lacuna de informações sobre a relação entre a distribuição das espécies de lagartos e serpentes na Amazônia Brasileira em relação a fatores ecológicos, esta tese tem como objetivo avaliar a influência de variáveis ambientais, climáticas e estruturais da vegetação na composição, riqueza e abundância dessas espécies em diferentes escalas espaciais e temporais. No primeiro capítulo, investigamos os padrões temporais e as respostas das comunidades de lagartos e serpentes ao longo de nove anos de amostragens RAPELD em diferentes ambientes na Floresta Nacional de Carajás, uma área que combina floresta amazônica com formações de savana metalófila (canga). No segundo capítulo, avaliamos a influência de variáveis ambientais na composição de comunidades de Squamata em 13 áreas, distribuídas em diferentes regiões biogeográficas da bacia Amazônica, utilizando dados coletados em expedições a campo pelo sistema RAP. Por fim, no terceiro capítulo, investigamos como diferentes métodos de amostragem afetam as estimativas de diversidade taxonômica e

funcional de lagartos e serpentes, fornecendo percepções importantes para o planejamento de futuros estudos e programas de monitoramento.

2. OBJETIVOS

i. Objetivo Geral

Investigar o papel dos gradientes ambientais, dinâmica temporal e métodos de amostragem na estruturação da diversidade taxonômica e funcional de assembleias de lagartos e serpentes na Amazônia brasileira.

ii. Objetivos Específicos

Capítulo 1 – *Temporal Patterns in Lizard and Snake Communities: Contrasting Responses to Environmental Factors in Carajás National Forest*

Objetivos: 1) Analisar a influência de variáveis ambientais (vegetação, elevação do terreno, temperatura e umidade) na composição, abundância e riqueza das assembleias de lagartos e serpentes na Floresta Nacional de Carajás. 2) Examinar as tendências temporais dos parâmetros comunitários (riqueza e abundância) de lagartos e serpentes, considerando variações no esforço de amostragem no período de 2015 a 2023. 3) Compreender as relações entre os gradientes ambientais e a dinâmica das comunidades de lagartos e serpentes, evidenciando implicações ecológicas relevantes para a conservação do ecossistema estudado.

Capítulo 2 – *Environmental Influence on the Composition of Squamata Assemblages in the Brazilian Amazon*

Objetivos: 1) Identificar quais variáveis ambientais, estruturais e climáticas, influenciam significativamente a riqueza de espécies de lagartos e serpentes em 13 áreas de floresta no bioma Amazônico. 2) Determinar como essas variáveis ambientais afetam a abundância de lagartos e serpentes nas áreas amostradas. 3) Avaliar como a estrutura ambiental e o clima moldam a composição das comunidades de lagartos e serpentes em diferentes regiões da Amazônia brasileira.

Capítulo 3 – *Sampling Method Effects on Taxonomic and Functional Diversity Patterns of Lizards and Snakes in the Brazilian Amazon*

Objetivos: 1) Comparar a eficácia de três métodos de amostragem – armadilhas de interceptação e queda (*Pitfall traps*), busca ativa e encontros ocasionais – na obtenção de estimativas de diversidade de lagartos e serpentes, evidenciando a complementaridade e os vieses específicos de cada técnica. 2) Determinar como a escolha dos métodos de amostragem influencia as estimativas

de diversidade utilizando números de Hill para riqueza, espécies comuns e dominantes e a composição de cada grupo. 3) Testar se as diferentes técnicas de amostragem afetam as medidas de diversidade funcional, avaliando se a gama de traços ecológicos dos répteis permanece consistente apesar das discrepâncias na detecção das diferentes espécies.

3. CAPÍTULO 1- Temporal and Environmental Variation in Squamate Assemblages Across Riparian and Terrestrial Habitats in the Brazilian Carajás Forest

Bruno Henrique V. de Miranda, Kauan Bassetto, Anderson da Rosa, Vitor Carvalho-Rocha, Selvino Neckel de Oliveira

ABSTRACT PAGE

Environmental heterogeneity plays a crucial role in structuring biological communities, particularly in regions with distinct habitat transitions such as those found in the Brazilian Carajás National Forest. This area features a particular mosaic of environments, including Amazonian rainforest and metalophilic savanna (*canga*), offering an excellent opportunity to study community responses to environmental gradients. We investigated how environmental variables influence squamate (lizards and snakes) community structure and examined temporal trends in these communities over nearly a decade (2015–2023). Standardized surveys were conducted in 68 plots across different vegetation types. We analyzed the effects of environmental predictors — vegetation structure, elevation, temperature, and humidity — on species abundance, richness, and composition using generalized linear models and redundancy analysis (RDA). Lizard communities exhibited strong responses to environmental gradients, with NDVI explaining approximately 41.7% of community variation and significantly influencing both abundance (adjusted $R^2 = 0.402$) and presence/absence patterns (adjusted $R^2 = 0.209$). In contrast, snake communities showed overall weaker responses (adjusted $R^2 \leq 0.021$), although elevation consistently influenced their distribution. Temporal analyses revealed contrasting trends: in forest habitats, lizard abundance showed a slight positive trend while lizard species richness tended to decline, suggesting that a few species may be becoming dominant. In riparian environments, lizards declined in abundance but exhibited a subtle increase in richness, and snake populations remained relatively stable despite lower detection rates. Our results underscore the critical role of environmental heterogeneity—particularly the interplay between forest structure and elevation gradients—in shaping squamate communities in the Carajás National Forest. The distinct responses observed between lizards and snakes emphasize the need for taxon-specific conservation strategies and long-term monitoring to better understand the ecological dynamics of these reptile communities.

Keywords: Amazon, Elevation, Environmental Gradients, Squamata, Temporal Dynamics, Vegetation Structure

1. INTRODUCTION

Understanding how environmental factors shape species distributions and community structure remains a fundamental challenge in ecology (Rosenzweig, 1995; Vellend, 2010). In tropical regions, where globally biodiversity reaches its peak, communities are often structured by complex interactions between abiotic conditions and species' physiological requirements and tolerances (Janzen, 1967; Sunday et al., 2011). Environmental filtering theory suggests that species persist in locations where their physiological optima match local environmental conditions, leading to non-random community assembly patterns across environmental gradients (Keddy, 1992; Weiher et al., 2011). This is especially relevant for ectothermic vertebrates, whose physiology and behavior are tightly linked to environmental conditions, unlike endotherms, which regulate body temperature through internal metabolic heat production (Angilletta, 2009; Huey & Kingsolver, 1989).

The role of environmental heterogeneity in maintaining biodiversity has been extensively studied in tropical forests (Jones et al., 2006; Valladares & Niinemets, 2008; de Fraga, 2018; Bitencourt, 2020; Maximiano, 2020). Local-scale environmental variation can create diverse microhabitats and resource gradients that support distinct species assemblages (Tews et al., 2004). Understanding how species respond to such environmental mosaics is crucial for predicting community responses to habitat modification and climate change (Yang et al., 2015). The complex interplay between environmental factors and species distributions remains a central theme in ecology, with significant implications for biodiversity conservation (Hubbell, 2005; Chase & Myers, 2011).

Lizards and snakes are particularly suitable for studying environmental effects on community structure due to their ectothermic metabolism and, therefore, strong associations with habitat characteristics (Pianka & Vitt, 2003; Vitt et al., 2007; Diele-Viegas & Rocha, 2018). Previous studies in Amazonia have shown that squamate communities respond to various environmental factors, including vegetation structure, microclimate, and topography (Pantoja & de Fraga, 2012; Faria et al., 2019; Massel et al., 2019 Peixoto et al., 2020). However, most of these studies have focused on broad-scale patterns, leaving gaps in our understanding of how environmental heterogeneity influences squamate communities at local scales, particularly in environments like the *canga* formations of Carajás National Forest.

The Carajás National Forest region in southeastern Pará represents a unique landscape with multiple environmental gradients within a continuous protected area, including variations in forest structure, topography, and habitat types. It is characterized by a mosaic of environments including ombrophilous forest and metalophilic savanna (*canga*), the latter being an uncommon ecosystem restricted to iron ore outcrops (Silva et al., 1996; Carvalho, 2010, Mota et al., 2018). This environmental heterogeneity provides an excellent opportunity to investigate how habitat characteristics and environmental gradients influence vertebrate communities at a local scale.

In this context, we aim to investigate how environmental variables influence

the structure of squamate communities in the Carajás National Forest region. We seek to understand how environmental gradients like vegetation cover, and elevation, along with microclimatic conditions (temperature and humidity) shape both the abundance and composition of these communities. In parallel, we examine the temporal trends in species richness and abundance, assessing how these community parameters vary annually from 2015 to 2023 while accounting for differences in sampling effort. By combining these two approaches, our research addresses both the spatial relationships between environmental variables and community structure as well as the long-term temporal dynamics in these parameters.

Understanding these patterns, including their spatial and temporal variability, is crucial for conservation planning in the Carajás region, especially given the ongoing mining activities and potential impacts of climate change. This study will contribute to our understanding of how environmental heterogeneity maintains biodiversity in this Amazonian landscape by integrating analyses of environmental drivers of community structure with long-term trends in species richness and abundance. Such a comprehensive approach provides valuable insights for developing management strategies that address both persistent environmental influences and emerging temporal shifts in lizard and snake communities.

2. METHODS

2.1. Study Site

The study was conducted in the Carajás National Forest (6°02'S, 50°17'W), located in southeastern Pará state, Brazil (Fig. 1). This protected area covers approximately 411,949 hectares and comprises a mosaic of environments, including ombrophilous forest and metalophilic savanna (*canga*). The climate is tropical humid (Aw according to Köppen classification), with a marked dry season from June to October and a rainy season from November to May. Annual rainfall averages 2,236 mm, with monthly precipitation varying from 382 mm in March to 26 mm in August. Mean annual temperature is 24°C, with daily temperatures ranging from 20.9°C to 28.9°C in the plateau areas (IBAMA, 2004; Tolbert et al., 1971).

The region is characterized by a series of discontinuous mountains and hills, with elevations ranging from 600 to 800 m. The plateaus are covered by iron ore outcrops and *canga* vegetation, while the surrounding valleys support dense rainforest. The formation of lateritic crust (*canga*) covering the plateaus has prevented the development of dense forest in these areas, creating distinct vegetation patches that contrast with the surrounding forest matrix (Silva et al., 1996; Tolbert et al., 1971, Mota et al., 2018).

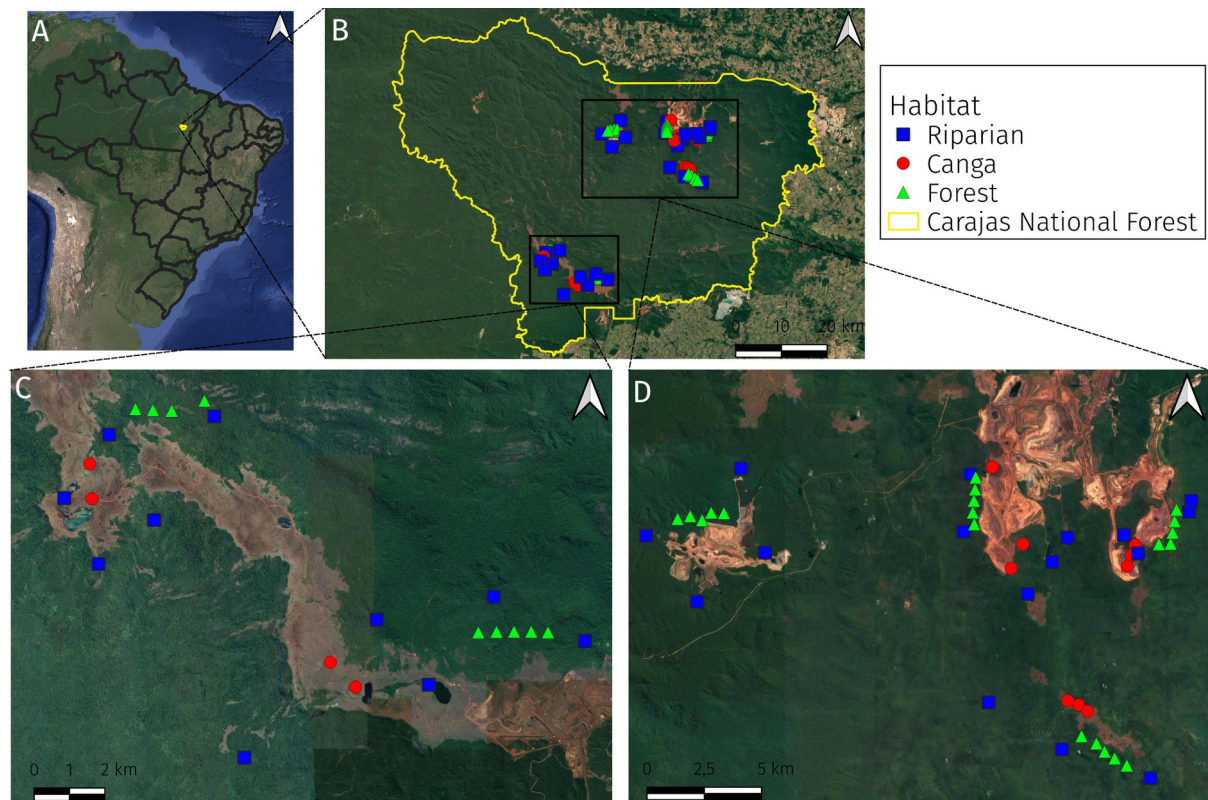


Figure 1. Study area and sampling transects in the Carajás National Forest, Brazil. (A) Brazil with location of study site; (B) Carajás National Forest boundary with sampling regions; (C) Detailed view of sampling points in Serra Sul; (D) Detailed view of sampling points in Serra Norte. Sampling points are color-coded by habitat type: blue for Riparian, red for Canga, and green for Forest. Scale bars indicate geographic distance.

2.2. Field Sampling and Specimen Processing

Data collection was conducted between 2015 and 2023 using a total of 68 sampling plots distributed across the Carajás National Forest, following the RAPELD (Rapid Assessment and Permanent Ecological Longitudinal Plots) sampling design (Magnusson, 2005). Of these 68 plots, 26 were consistently monitored throughout the entire eight-year period (Riparian), while 29 plots were sampled for five consecutive years (Forest), and 13 plots were sampled for 2 years (Canga).

Sampling was carried out during the rainy season (January to April) using standardized active search methods. Each plot features a 250-meter transect carefully positioned along the terrain's contour lines to minimize to minimize elevational, and thus environmental heterogeneity within each transect. Surveys were conducted during both day and night periods to maximize species detection across different activity periods, following established protocols for Amazonian herpetofauna (Martins & Oliveira, 1998; Bernarde et al., 2013; Ribeiro-Júnior et al., 2008).

We employed visual encounter surveys along the pre-established 250-meter transects, with two specialized herpetologists systematically searching all available microhabitats within 10 meters on each side of the transect line (Scott et al., 1994; Ribeiro-Júnior et al., 2008). Each sampling plot received a total of four hours/person

of sampling effort, with two specialists conducting independent surveys - one diurnal survey (15:30-18:00h) and one nocturnal survey (19:00-21:00h). All squamates encountered were identified to species level and their total abundance was recorded.

2.3. Environmental Variables

Five environmental variables were initially collected for each sampling plot: Normalized Difference Vegetation Index (NDVI), distance to the nearest *canga* formation (distcangam), elevation (elevm), temperature (temp), and humidity (umid). NDVI values for the corresponding sampling periods were derived from Landsat 8 satellite imagery (Fick & Hijmans, 2017). Distance from canga was calculated in QGIS (QGIS Development Team, 2023) as the shortest linear distance between each sampling point and the closest canga formation. Elevation data were extracted from digital elevation models (Lang et al., 2023). Temperature and humidity were recorded at each sampling event using digital thermohygrometers, adhering to standardized protocols (IBAMA, 2004).

2.4. Data Analysis

First, we examined correlations among predictor environmental variables using Spearman's rank correlation because collinearity among predictors can bias regression results. Due to strong correlations between distance from canga and both elevation ($r = -0.755$, $p < 0.001$) and NDVI ($r = 0.553$, $p < 0.001$), we excluded distance from canga from subsequent analyses (Table S8).

To assess the influence of the uncorrelated environmental variables (NDVI, elevation, temperature, and humidity) on squamate communities, we analyzed both abundance and richness patterns, as well as temporal trends. For abundance and richness analyses, we used generalized linear models (GLM) with negative binomial distribution for abundance data and Poisson distribution for richness data (Venables & Ripley, 2002).

To analyze community composition, we performed Redundancy Analysis (RDA) using abundance data transformed by the Hellinger method (Legendre & Gallagher, 2001). The significance of environmental variables in explaining community composition was tested using permutation tests with 999 iterations (Oksanen et al., 2020).

In our temporal trend analysis, we generated annual standardized metrics for both abundance and richness by accounting for differences in sampling effort. Specifically, for each year and environment type (riparian, forest and canga), we divided the total counts and species richness by the number of distinct sampling units (transects) visited. This standardization was applied to data grouped by two squamate suborders (lizards and snakes) over the study period (2015–2023). We then modeled temporal trends using generalized linear models: a negative binomial (with a fallback to Poisson when necessary) for the abundance data and a Poisson model for the richness data, both of which incorporated log-transformed offsets to adjust for sampling effort.

All analyses were performed in R (version 4.2.2) using the following packages:

tidyverse (Wickham et al., 2019), for data transformation; MASS (Venables & Ripley, 2002) for fitting generalized linear models; broom (Robinson et al., 2023) for extracting model summaries; and cowplot (Wilke, 2020) and ggplot2 (Wickham, 2016) for visualization. In addition, supplementary tables provide descriptive summaries of abundance, richness, and sampling effort, thereby ensuring a comprehensive view of our dataset (Supplementary Material).

3. RESULTS

3.1 - Species Richness and Abundance

In our study at the Carajás National Forest, we recorded a total of 16 lizard species and 40 snake species (Table S1, Supplementary Material). Among the lizards, the most abundant species were *Chatogekko amazonicus*, with 1,118 individuals (mean abundance per site of 21.1), followed by *Tropidurus oreadicus*, with 130 individuals (mean of 7.65 per transect), and *Neusticurus bicarinatus*, with 83 individuals (mean of 5.19 per transect). These species exhibited a detection rate of 100%, indicating their consistent occurrence across the surveyed sites. In the snake assemblage, the most abundant were *Dipsas catesbyi* (38 individuals recorded at 19 sites), *Leptodeira annulata* (22 individuals at 18 sites), and *Siphlophis compressus* (12 individuals at 7 sites).

3.2 - Environmental Effects on Abundance and Richness

Lizard species abundance increased significantly with vegetation cover (NDVI, a proxy for vegetation cover), showing a strong positive effect ($\beta = 0.391$, $p = 0.002$). In contrast, elevation, temperature, and humidity did not affect the abundance of lizards. Lizard species richness was positively associated with NDVI ($\beta = 0.257$, $p = 0.015$), suggesting that increased vegetation cover favors the presence of more species. However, there was a negative relationship with elevation ($\beta = -0.204$, $p = 0.020$), which may indicate that higher elevations could constrain species richness. Temperature and humidity had negligible effects on lizard richness.

For snakes, abundance was strongly influenced by elevation ($\beta = -0.502$, $p < 0.001$), indicating that snake abundance is higher at lower elevations. Similarly, snake richness exhibited a strong negative relationship with elevation ($\beta = -0.442$, $p < 0.001$), while the other environmental variables did not have significant effects on snake community parameters.

The relative importance of these predictors differed between the groups and response variables (Tables S2 & S3, Supplementary Material). For lizard abundance and richness, NDVI was consistently the most important predictor, with importance values of 0.908 and 0.929, respectively. In the case of snakes, elevation emerged as the dominant factor for both abundance and richness, with an importance value of 1.000. These patterns underscore the differential roles that vegetation structure and topographic gradients play in structuring squamate communities in the Carajás National Forest.

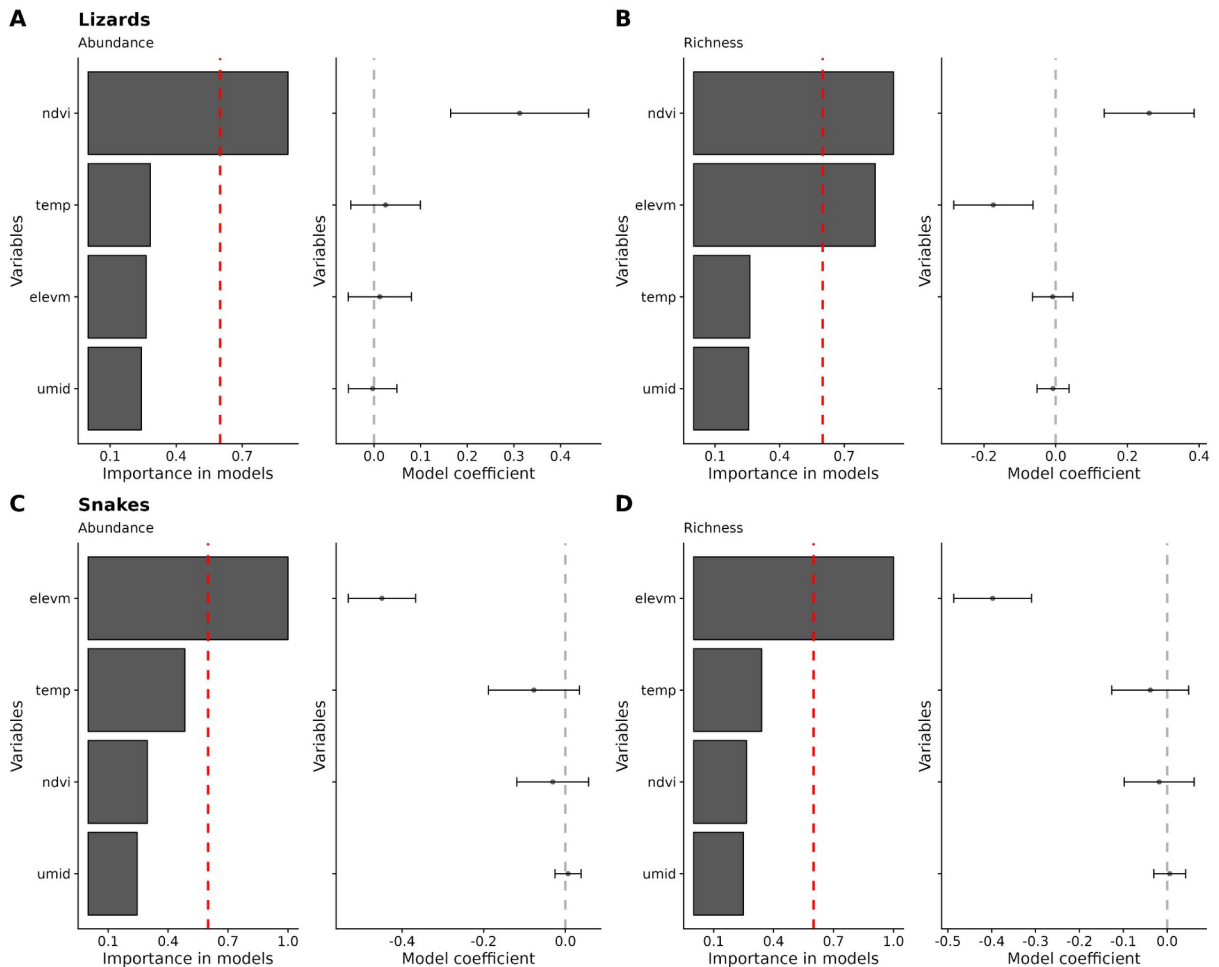


Figure 2: Relative importance of environmental variables in the best-fitting models for (A) Lizard abundance, (B) Lizard richness, (C) Snake abundance, and (D) Snake richness. Left panels show the relative importance of variables in models, with vertical red lines indicating the importance threshold (importance > 0.6). Right panels show model coefficients with confidence intervals, indicating positive or negative effects of variables. Variables tested: Normalized Difference Vegetation Index (NDVI), Temperature (temp), Elevation (elevm), and Humidity (umid).

3.3 - Community Composition Analysis

Lizard community structure based on abundance data showed 43.7% of total variation explained by the RDA (adjusted $R^2 = 0.401$) (Table S4 & S6, Supplementary Material). The first two constrained axes accounted for approximately 41.7% and 1.7% of the total variation, respectively. The global permutation test was highly significant ($F = 12.21$, $p = 0.001$), indicating a strong relationship between environmental variables and lizard abundance. Among the environmental predictors, NDVI emerged as the strongest factor ($F = 44.82$, $p = 0.001$), followed by elevation ($F = 3.39$, $p = 0.029$); temperature and humidity did not show effects (Figure 3, Table S5).

When the analysis was based on lizard presence/absence data, environmental variables explained 25.0% of the variation (adjusted $R^2 = 0.209$). The global model remained highly significant, with a permutation test yielding $F = 5.25$ ($p = 0.001$). In this configuration, both NDVI ($F = 15.52$, $p = 0.001$) and elevation ($F =$

4.54, $p = 0.001$) had significant impacts, while temperature and humidity showed negligible effects. The first RDA axis explained roughly 21% of the total variation, underscoring a strong environmental gradient structuring lizard community composition on the basis of species occurrence.

Snake communities, in contrast, exhibited weaker relationships with environmental predictors. For abundance data, the constrained model explained only 10.1% of the total variation, with an adjusted R^2 of 0.024. The global test was marginally significant ($F = 1.31$, $p = 0.035$). The terms test indicated a significant effect of NDVI ($F = 1.75$, $p = 0.031$) while elevation, temperature, and humidity had less pronounced effects (e.g., elevation with $F = 1.46$, $p = 0.079$). The first two RDA axes for snake abundance explained approximately 3.9% and 2.7% of the total variation, respectively.

For snake presence/absence data, environmental variables explained a similar low proportion of the variation (adjusted $R^2 = 0.020$), and the global model was not significant ($F = 1.31$, $p = 0.115$). However, when considering individual predictors, elevation emerged as a significant factor ($F = 2.12$, $p = 0.004$), while NDVI, temperature, and humidity did not exert significant influences. The comparatively low explanatory power for snake communities indicates that other unmeasured factors may be more important in structuring these assemblages.

Species–environment relationships remained evident despite the overall lower variance explained for snakes. Among lizards, for example, *Chatogekko amazonicus* showed a strong association with NDVI, while *Tropidurus oreadicus* was more closely associated with higher elevation. For snakes, although species associations with environmental gradients were less pronounced, elevation emerged as a key predictor, suggesting that topographic gradients are more influential in determining snake distribution patterns.

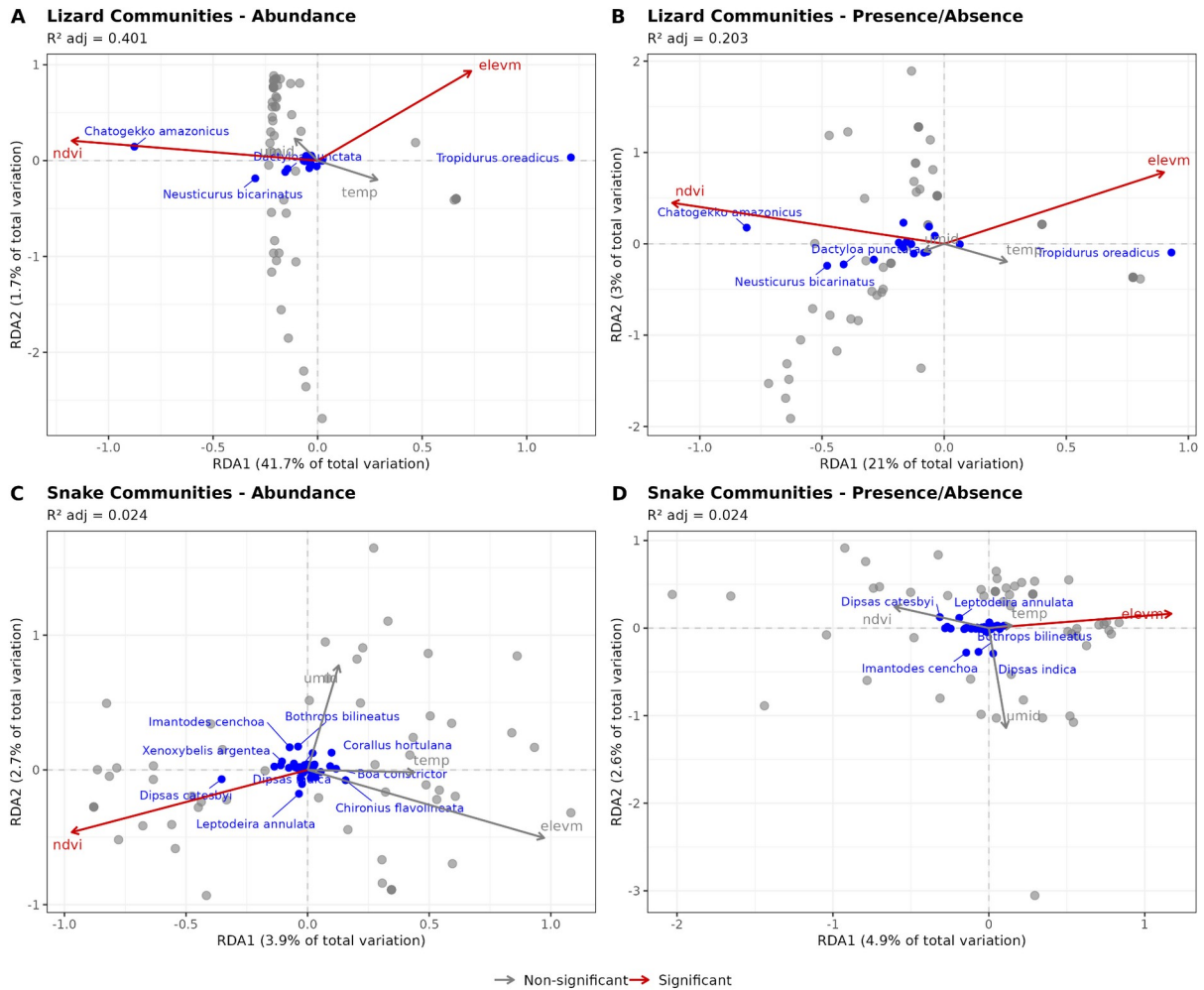


Figure 3: Redundancy Analysis (RDA) ordination plots showing the relationship between environmental variables and reptile communities. (A) Lizard communities based on abundance data (R^2 adj = 0.401); (B) Lizard communities based on presence/absence data (R^2 adj = 0.203); (C) Snake communities based on abundance data (R^2 adj = 0.024); (D) Snake communities based on presence/absence data (R^2 adj = 0.024). Gray dots represent sampling sites, blue dots represent species, and arrows indicate environmental variables (red arrows = significant, gray arrows = non-significant). Environmental variables tested were: Normalized Difference Vegetation Index (ndvi), Temperature (temp), Elevation (elevm), and Humidity (umid). The percentage of total variation explained by each RDA axis is shown in parentheses.

3.3 - Temporal Patterns in Abundance and Richness

Standardized abundance and richness analyses revealed variations in lizard and snake communities across forest and riparian environments from 2015 to 2023. Although no statistically significant trends were detected, some patterns emerged. In forest environments, lizard communities showed a slight positive trend in abundance (0.2236 per year, $p = 0.0857$), contrasting with a marginal negative trend for snake communities (-0.0284 per year, $p = 0.8011$). Riparian areas presented an inverse pattern, with lizards displaying a minor decline in abundance (-0.0265 per year, $p = 0.3453$), while snakes exhibited a slight increase (0.0188 per year, $p = 0.6151$) (Table S7, Supplementary Material).

Species richness patterns showed similar subtle variations: forest environments indicated a slight decline for both lizards (-0.0302 per year, $p = 0.8383$) and snakes (-0.0733 per year, $p = 0.6073$), with the latter showing a more pronounced reduction. Riparian areas demonstrated more stable richness patterns, with lizards showing a minimal increase (0.0160 per year, $p = 0.7671$) and snake richness remaining nearly constant (-0.0056 per year, $p = 0.9015$). The canga habitat presented insufficient data for comprehensive analysis, underscoring the need for more extensive sampling in this unique environmental context.

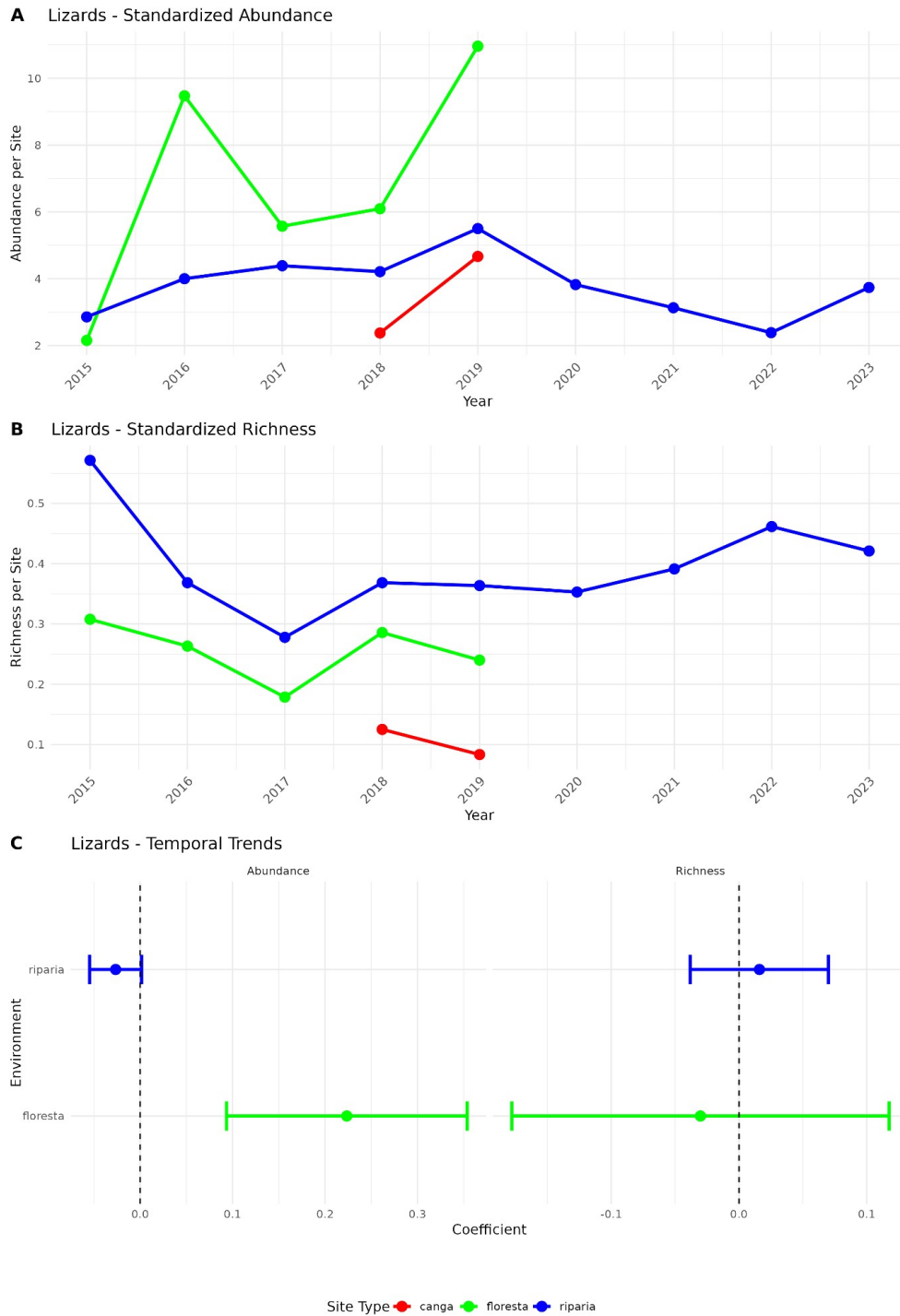


Figure 4: Temporal patterns of lizard communities across different site types from 2015 to 2023. (A) Standardized abundance per site, showing variations across riparian (blue), forest (green), and canga (red) environments. (B) Standardized species richness per site, illustrating differences in species diversity across site types. (C) Temporal trends showing coefficients of abundance and richness for each environment, with error bars representing confidence intervals. Site types are color-coded: canga (red), forest (green), and riparian (blue).

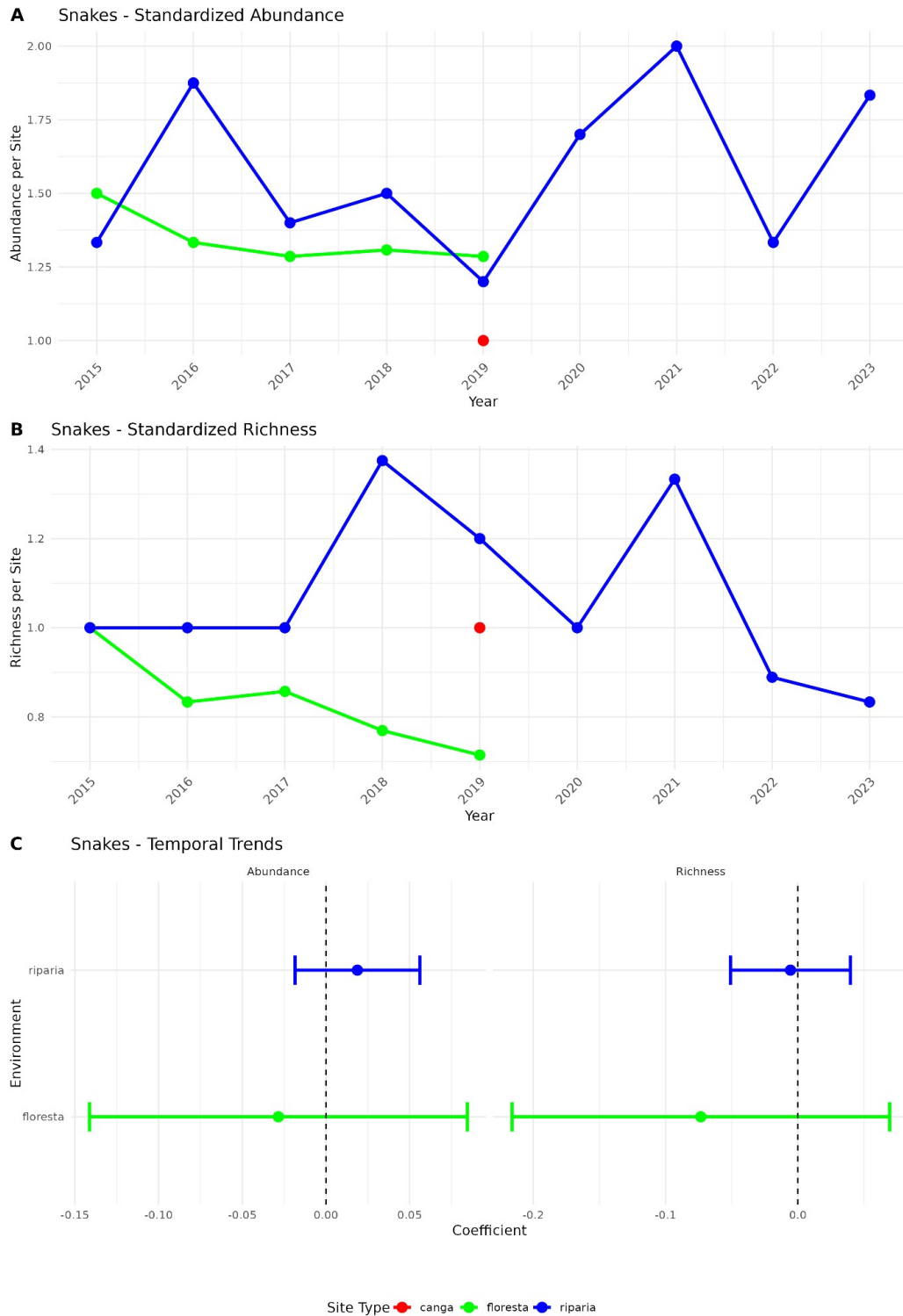


Figure 4: Temporal patterns of snake communities across different site types from 2015 to 2023. (A) Standardized abundance per site, showing variations across riparian (blue), forest (green), and canga (red) environments. (B) Standardized species richness per site, illustrating differences in species diversity across site types. (C) Temporal trends showing coefficients of abundance and richness for each environment, with error bars representing confidence intervals. Site types are color-coded: canga (red), forest (green), and riparian (blue).

4. DISCUSSION

Our study revealed distinct patterns in how environmental variables and temporal dynamics influence squamate communities in the Carajás National Forest region. After accounting for correlations among environmental predictors, we found that lizard communities showed stronger responses to vegetation structure and elevation, while snake communities exhibited weaker yet detectable responses to elevation. These findings align with previous studies in the Amazon that have demonstrated the importance of vegetation structure and topographic variables in shaping reptile communities (Fraga *et al.*, 2011; Faria *et al.*, 2019; Masseli *et al.*, 2019; Peixoto *et al.*, 2020).

The strong association between lizard communities and NDVI (explaining 41.7% of community variation) suggests that vegetation structure plays a crucial role in determining lizard distribution and abundance. This relationship likely reflects the importance of thermal microhabitats and refuge availability, as demonstrated in other tropical forest systems (Diele-Viegas & Rocha, 2018; Shah *et al.*, 2017). The additional influence of elevation on lizard communities, particularly for species richness, indicates that topographic heterogeneity contributes to maintaining lizard diversity through environmental gradients characteristic of the Carajás region (Silva *et al.*, 1996; Carvalho, 2010). In Carajás, elevation gradients create a unique environmental transition: higher elevations feature metalophilic savanna formations ("canga") characterized by exposed ferruginous outcrops, harsher microclimatic conditions (higher temperatures, lower humidity), and more open vegetation structure (Campos, 2012). These cangas harbor specialized heliophilic lizard species that prefer direct sun exposure (*Tropidurus oreadicus*), resulting in less diverse but highly specialized assemblages. In contrast, lower elevations support dense forest formations with higher humidity, more complex vegetation structure, and greater microhabitat diversity, fostering richer lizard communities dominated by forest-dwelling species (e.g., *Chatogekko amazonicus*, *Neusticurus bicarinatus*, *Cercosaura ocellata*) and arboreal species (e.g., *Dactyloa punctata*, *Thecadactylus rapicauda*). This elevation-driven habitat transition creates distinct lizard assemblages across relatively short geographic distances, highlighting the conservation importance of protecting the full elevational range within the Carajás complex."

In forest habitats, our analyses indicate that lizard abundance showed a slight positive trend—possibly reflecting increasingly favorable environmental conditions, habitat recovery or expansion, and reduced predation or competition—while the slight decline in species richness may suggest that a few species are becoming increasingly dominant or specialized. This pattern is particularly evident in the dominance of *Chatogekko amazonicus*, which represented over 94% of all lizard captures in forest habitats. This small gecko's success likely stems from its efficient exploitation of leaf litter microhabitats in the forest floor and its ability to remain active throughout the day, despite not engaging in basking behavior typical of many lizards. While abundant in undisturbed forests, its sensitivity to forest fragmentation suggests

that the observed dominance may reflect habitat integrity in our sampled areas (Gamble, 2011). Other species recorded in forest areas, such as *Cercosaura ocellata*, *Dactyloa punctata*, and *Gonatodes humeralis*, occurred at much lower abundances, suggesting potential niche partitioning or competitive exclusion. For snake communities in forested areas, the observed declines in both abundance and richness point to potential impacts of habitat fragmentation and microclimatic alterations. The most frequently recorded species were *Dipsas catesbyi* and *Leptodeira annulata*, both nocturnal arboreal specialists with specialized diets (mollusks and amphibians, respectively), suggesting that forest structural integrity and prey availability are critical factors for maintaining snake diversity in these areas.

In riparian environments, contrasting dynamics were evident. Lizards exhibited a decline in abundance that may be associated with changes in hydrological regimes, modifications in marginal vegetation, or increasing anthropogenic pressures. The community structure in these environments was dominated by *Chatogekko amazonicus* and *Neusticurus bicarinatus*, which together accounted for approximately 77% of all lizard captures in riparian habitats. While *C. amazonicus* is a leaf litter specialist with hydrophobic skin that facilitates occupation of humid microhabitats despite not being aquatic (Gamble, 2011), *N. bicarinatus* displays the characteristic 'Crocodile-Like Morphology' (CLM) with adaptations for semi-aquatic life. These include lateral tail compression, double caudal crest, and heterogeneous dorsal scalation with enlarged tubercles—all morphological features that enhance swimming performance in aquatic environments (Marques-Souza, 2017). *N. bicarinatus* individuals are typically found near stream edges, where they forage and take refuge, often resting on branches above the water at night (Ávila-Pires, 1995). The subtle increase in species richness, despite declining abundance, suggests potential niche diversification in riparian zones. For snake communities in riparian habitats, the slight increase in abundance and near stability in species richness suggest greater resilience, likely linked to a more consistent availability of prey resources and lower susceptibility to seasonal disturbances. Riparian snake assemblages showed higher diversity than forest communities, with *Dipsas catesbyi*, *Leptodeira annulata*, and *Siphlophis compressus* being most abundant. Notably, the presence of *Helicops angulatus*, an aquatic specialist that feeds primarily on fish and amphibians, highlights the importance of water resources in structuring these communities. Although these temporal trends are marginal and not statistically significant, they highlight the complex ecological responses across different habitats.

It is important to underscore that long-term monitoring of reptiles is rare, and our temporal analyses—spanning nearly a decade from 2015 to 2023—provide valuable insights into trends that are seldom documented for these taxa. The marginal yet contrasting trends in forest and riparian habitats emphasize that even in systems that appear relatively stable, subtle changes may be underway. These findings call for continuous monitoring and further investigations to distinguish between natural fluctuations and potential shifts driven by environmental change (Moraes et al., 2016; Peixoto et al., 2023; Sunday et al., 2011).

Our findings have important implications for conservation planning in the

Carajás region. The strong influence of vegetation structure on lizard communities suggests that maintaining forest integrity is crucial for preserving squamate diversity. Additionally, the importance of elevation gradients in structuring both lizard and snake communities emphasizes the need to protect the full range of topographic variation in the landscape, particularly given ongoing mining activities in the region (Martins et al., 2012; Peixoto et al., 2023). Several limitations should be considered when interpreting our results. First, lower detection rates for snakes likely resulted in underestimated diversity patterns—a common challenge in snake studies (Durso et al., 2011; de Fraga et al., 2014). Second, variation in sampling effort across years, though accounted for in our analyses, may have influenced our ability to detect subtle temporal trends. Future studies would benefit from more consistent long-term monitoring protocols and the incorporation of detection probability models (MacKenzie & Kendall, 2002; Mazerolle et al., 2007).

In summary, the complex interactions between environmental variables and squamate communities in the Carajás National Forest underline the importance of maintaining environmental heterogeneity. Our study reveals that vegetation structure and elevation are primary drivers of community organization, yet their effects vary markedly between lizards and snakes. As mining activities and climate change continue to shape this landscape, understanding these differential responses becomes increasingly crucial for developing effective, taxon-specific conservation strategies. Future research should focus on elucidating the underlying mechanisms of these patterns and expanding long-term studies of reptile communities in this unique Amazonian ecosystem.

5. CONCLUSION

Our study provides evidence for the complex relationships between environmental heterogeneity and squamate communities in the Carajás National Forest. The distinct responses of lizards and snakes to environmental gradients, coupled with temporal trends in their populations observed over nearly a decade, underscore the importance of maintaining habitat diversity in this unique Amazonian landscape. The strong influence of vegetation structure (NDVI) on lizard communities and the consistent effects of elevation on both groups suggest that conservation strategies should prioritize the preservation of these critical environmental gradients. Our analyses revealed that while these predictors are often correlated, they influence squamate communities through different mechanisms—lizards respond primarily to vegetation structure, whereas snakes appear to be more affected by topographic variation. As mining activities and climate change continue to impact the region, long-term monitoring of these reptile communities will be essential for understanding and mitigating potential negative effects on biodiversity. Future research should focus on developing more robust sampling protocols for cryptic species and further investigating the mechanisms underlying these differential responses. Importantly, the integration of spatial and temporal analyses in our study contributes to the growing body of evidence supporting the critical role of environmental heterogeneity in maintaining biodiversity in human-modified landscapes and provides valuable insights for taxon-specific conservation planning in the Amazon-Cerrado ecotone.

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7. Supplementary Material

Table S1 - Species list and abundance data for squamates (lizards and snakes) recorded in the Carajás National Forest, Brazil. Total_Abundance represents the total number of individuals recorded for each species across all sampling sites. N_Sites_Total indicates the total number of sampling sites where each species was recorded. N_Sites_Canga, N_Sites_Forest, and N_Sites_Riparian show the number of sites of each habitat type (canga outcrop, forest, and riparian areas, respectively) where each species was detected. Abundance Canga, Abundance Forest, and Abundance Riparian display the total number of individuals recorded in each habitat type. Species are arranged by taxonomic group (Lizard/Snake) and decreasing total abundance within each group.

Squamate	Species	Total Abundance	N_Sites Total	N_Sites Canga	N_Sites Forest	N_Sites Riparian	Abundance Canga	Abundance Forest	Abundance Riparian
Lizard	<i>Chatogekko amazonicus</i>	1118	53	0	29	24	0	724	394
Lizard	<i>Tropidurus oreadicus</i>	130	17	13	1	3	75	1	54
Lizard	<i>Neusticurus bicarinatus</i>	83	16	0	0	16	0	0	83
Lizard	<i>Potamites ecpleopus</i>	36	12	0	0	12	0	0	36
Lizard	<i>Dactyloa punctata</i>	17	14	0	4	10	0	5	12
Lizard	<i>Cercosaura</i>	16	10	0	8	2	0	14	2

	<i>ocellata</i>								
Lizard	<i>Thecadactylus rapicauda</i>	15	8	0	4	4	0	5	10
Lizard	<i>Norops fuscoauratus</i>	9	7	0	1	6	0	3	6
Lizard	<i>Kentropyx calcarata</i>	7	6	0	1	5	0	1	6
Lizard	<i>Gonatodes humeralis</i>	5	4	0	4	0	0	5	0
Lizard	<i>Plica plica</i>	5	5	0	1	4	0	1	4
Lizard	<i>Plica umbra</i>	5	4	0	1	3	0	1	4
Lizard	<i>Enyalius leechii</i>	4	4	0	4	0	0	4	0
Lizard	<i>Copeoglossum nigropunctatum</i>	3	3	0	2	1	0	2	1
Lizard	<i>Ameiva ameiva</i>	2	2	0	0	2	0	0	2
Lizard	<i>Uranoscodon superciliosus</i>	1	1	0	0	1	0	0	1
Snake	<i>Dipsas catesbyi</i>	38	19	0	9	10	0	15	23
Snake	<i>Leptodeira annulata</i>	22	18	0	6	12	0	7	15

Snake	<i>Siphlophis compressus</i>	12	7	0	1	6	0	1	11
Snake	<i>Imantodes cenchoa</i>	9	8	0	3	5	0	4	5
Snake	<i>Bothrops bilineatus</i>	8	7	0	2	5	0	2	6
Snake	<i>Helicops angulatus</i>	8	4	0	0	4	0	0	8
Snake	<i>Xenoxybelis argentea</i>	7	7	0	2	5	0	2	5
Snake	<i>Oxyrhopus petolarius</i>	6	3	0	0	3	0	0	6
Snake	<i>Anilius scytale</i>	4	4	0	0	4	0	0	4
Snake	<i>Corallus batesii</i>	4	4	0	1	3	0	1	3
Snake	<i>Micrurus paraensis</i>	4	4	0	3	1	0	3	1
Snake	<i>Oxybelis aeneus</i>	4	3	0	2	1	0	2	2
Snake	<i>Oxyrhopus melanogenys</i>	4	4	0	4	0	0	4	0
Snake	<i>Bothrops</i>	3	3	0	1	2	0	1	2

	<i>taeniatus</i>								
Snake	<i>Chironius scurrulus</i>	3	2	0	0	2	0	0	3
Snake	<i>Dendrophidion dendrophis</i>	3	3	0	1	2	0	1	2
Snake	<i>Phrynonax poecilonotus</i>	3	3	0	1	2	0	1	2
Snake	<i>Atractus tartarus</i>	2	2	0	0	2	0	0	2
Snake	<i>Boa constrictor</i>	2	2	1	0	1	1	0	1
Snake	<i>Corallus hortulana</i>	2	2	1	0	1	1	0	1
Snake	<i>Drepanoides anomalus</i>	2	2	0	0	2	0	0	2
Snake	<i>Pseudoboa coronata</i>	2	1	0	0	1	0	0	2
Snake	<i>Xenopholis scalaris</i>	2	2	0	0	2	0	0	2
Snake	<i>Chironius exoletus</i>	1	1	0	0	1	0	0	1
Snake	<i>Chironius</i>	1	1	1	0	0	1	0	0

	<i>flavolineata</i>								
Snake	<i>Chironius fuscus</i>	1	1	0	0	1	0	0	1
Snake	<i>Dipsas indica</i>	1	1	0	0	1	0	0	1
Snake	<i>Dipsas variegata</i>	1	1	0	1	0	0	1	0
Snake	<i>Drymoluber dichorus</i>	1	1	0	1	0	0	1	0
Snake	<i>Epicrates cenchria</i>	1	1	0	1	0	0	1	0
Snake	<i>Lachesis muta</i>	1	1	0	0	1	0	0	1
Snake	<i>Micrurus hemprichii</i>	1	1	0	1	0	0	1	0
Snake	<i>Micrurus surinamensis</i>	1	1	0	0	1	0	0	1
Snake	<i>Pseudoboa nigra</i>	1	1	0	1	0	0	1	0
Snake	<i>Rhinobothryum lentiginosum</i>	1	1	0	0	1	0	0	1
Snake	<i>Sibon nebulatus</i>	1	1	0	0	1	0	0	1

Snake	<i>Siphlophis worontzowi</i>	1	1	0	0	1	0	0	1
Snake	<i>Spilotes sulphureus</i>	1	1	0	0	1	0	0	1
Snake	<i>Taeniophallus quadriocellatus</i>	1	1	0	0	1	0	0	1
Snake	<i>Trilepida macrolepis</i>	1	1	0	0	1	0	0	1

Table S2 - Model selection results for abundance and species richness of lizards and snakes in the Brazilian Amazon. Models with $\Delta\text{AICc} < 2$ are shown for each group and response variable. Environmental predictors included: Normalized Difference Vegetation Index (ndvi), elevation (elevm), temperature (temp), and humidity (umid). For each model, we present the degrees of freedom (df), log-likelihood (logLik), Akaike Information Criterion corrected for small sample sizes (AICc), difference in AICc from the best model (delta), and Akaike weight (weight).

Group	Response	Model	Variables	df	logLik	AICc	delta	weight
Lizard	Abundance	1	(Intercept) + ndvi	3	-273.608	553.591	0.000	0.715
Lizard	Abundance	2	(Intercept) + ndvi + temp	4	-273.399	555.432	1.841	0.285
Lizard	Richness	1	(Intercept) + elevm + ndvi	3	-108.193	222.761	0.000	0.001
Snake	Abundance	1	(Intercept) + elevm	3	-95.550	197.599	0.000	0.44
Snake	Abundance	2	(Intercept) + elevm + temp	4	-94.571	197.993	0.394	0.361
Snake	Abundance	3	(Intercept) + elevm + ndvi + temp	5	-93.942	199.189	1.59	0.199
Snake	Richness	1	(Intercept) + elevm	2	-82.484	169.213	0.000	0.67
Snake	Richness	2	(Intercept) + elevm + temp	3	-82.064	170.627	1.414	0.33

Table S3 - Relative importance of environmental variables in explaining abundance and richness patterns for lizards and snakes separately. Values represent the sum of Akaike weights for all models containing each variable, providing a measure of variable importance in the model selection framework. Variables with importance values > 0.6 are considered to have strong support.

Group	Response	Variable	Importance
Lizard	Abundance	ndvi	0.908
Lizard	Abundance	temp	0.283
Lizard	Abundance	elevm	0.264
Lizard	Abundance	umid	0.242
Lizard	Richness	ndvi	0.929
Lizard	Richness	elevm	0.844
Lizard	Richness	temp	0.262
Lizard	Richness	umid	0.256
Snake	Abundance	elevm	0.001
Snake	Abundance	temp	0.484
Snake	Abundance	ndvi	0.297
Snake	Abundance	umid	0.245
Snake	Richness	elevm	0.001
Snake	Richness	temp	0.34
Snake	Richness	ndvi	0.265
Snake	Richness	umid	0.249

Table S4 - Overall model results showing adjusted R^2 values, global F-statistics, and significance levels for each analysis. Analyses were conducted separately for lizard and snake communities, using both abundance data (Hellinger-transformed) and

presence/absence data.

Analysis	R2_adj	Global_F	Global_p
Lizard Communities - Abundance	0.401	12.2	0,001
Lizard Communities - Presence/Absence	0.203	5.25	0,001
Snake Communities - Abundance	0.024	1.31	0,035
Snake Communities - Presence/Absence	0.024	1.31	0,089

Table S5 - Individual environmental variable results showing F-statistics and p-values for each predictor variable (NDVI, elevation, temperature, and humidity) across different analyses. Significant relationships ($p < 0.05$) are indicated in bold.

Analysis	Variable	F_value	P_value
Lizard Communities - Abundance	ndvi	44.82	0,001
Lizard Communities - Abundance	elevm	3.39	0,029
Lizard Communities - Abundance	temp	0.15	0,974
Lizard Communities - Abundance	umid	0.46	0,615
Lizard Communities - Presence/Absence	ndvi	15.52	0,001
Lizard Communities - Presence/Absence	elevm	4.54	0,001
Lizard Communities - Presence/Absence	temp	0.3	0,974
Lizard Communities - Presence/Absence	umid	0.66	0,676
Snake Communities - Abundance	ndvi	1.75	0,31
Snake Communities - Abundance	elevm	1.46	0,79
Snake Communities - Abundance	temp	0.91	0,571
Snake Communities - Abundance	umid	1.14	0,343
Snake Communities - Presence/Absence	ndvi	1.29	0,164
Snake Communities - Presence/Absence	elevm	2.12	0,003

Snake Communities - Presence/Absence	temp	0.51	0,942
Snake Communities - Presence/Absence	umid	1.33	0,183

Table S6 - RDA axis results showing the percentage of variation explained by each axis, along with F-statistics and p-values. Results are shown for the first two RDA axes of each analysis.

Analysis	Axis	Variation_Explained	F_value	P_value
Lizard Communities - Abundance	RDA1	41.67	46.6	0,001
Lizard Communities - Abundance	RDA2	1.67	1.87	0,478
Lizard Communities - Presence/Absence	RDA1	21.0	17.64	0,001
Lizard Communities - Presence/Absence	RDA2	2.96	2.49	0,165
Snake Communities - Abundance	RDA1	3.93	2.05	0,138
Snake Communities - Abundance	RDA2	2.66	1.39	0,521
Snake Communities - Presence/Absence	RDA1	4.92	2.57	0,71
Snake Communities - Presence/Absence	RDA2	2.65	1.38	0,598

Table S7 - Temporal trend coefficients for squamate abundance and species richness from 2015 to 2023 in the Carajás National Forest. Results are presented separately for lizards and snakes, and for two environments: “floresta” (forest) and “riparia” (riparian). The “estimate” represents the slope of the temporal trend (per year) derived from models that account for differences in sampling effort using offset terms. Columns “std.error” and “statistic” report the standard error and Z-statistic of each trend estimate, respectively, while “p.value” indicates the significance level of the trend. ‘ns’ denotes trends that are not statistically significant.

Group	Environment	metric	estimate	std.error	statistic	p.value	significance
Lizards	floresta	Abundance	0.2236	0.1301	1.7188	0.0857	ns
Lizards	floresta	Richness	-0.0302	0.1478	-0.2041	0.8383	ns
Lizards	riparia	Abundance	-0.0265	0.0281	-0.9438	0.3453	ns
Lizards	riparia	Richness	0.0016	0.0541	0.2962	0.7671	ns

Snakes	floresta	Abundance	-0.0284	0.1128	-0.2519	0.8011	ns
Snakes	floresta	Richness	-0.0733	0.1427	-0.5139	0.6073	ns
Snakes	riparia	Abundance	0.0188	0.0373	0.5028	0.6151	ns
Snakes	riparia	Richness	-0.0056	0.0453	-0.1238	0.9015	ns

Table S8 - Spearman's rank correlation coefficients between environmental variables measured in the Carajás National Forest. Variables analyzed were: Normalized Difference Vegetation Index (ndvi), distance to canga formations (distcangam), elevation (elevm), temperature (temp), and humidity (umid). Correlation values range from -1 to 1. P_value indicates the statistical significance of each correlation, with significance levels shown as: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, . $p < 0.1$, ns = not significant ($p > 0.1$). The strong correlation between distcangam and elevm (-0.676, $p < 0.001$) led to the exclusion of distcangam from subsequent analyses to avoid multicollinearity issues.

Variable1	Variable2	Correlation	P_value	Significance
ndvi	distcangam	0.319	<0.001	***
ndvi	elevm	-0.327	<0.001	***
ndvi	temp	-0.082	0.118	ns
ndvi	umid	0.061	0.251	ns
distcangam	elevm	-0.676	<0.001	***
distcangam	temp	0.025	0.634	ns
distcangam	umid	0.033	0.529	ns
elevm	temp	-0.102	0.053	.
elevm	umid	0.016	0.757	ns
temp	umid	-0.186	<0.001	***

4. CAPÍTULO 2 - Environmental influence on the composition of Squamata assemblages in the Brazilian Amazon

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ABSTRACT PAGE

Understanding the environmental factors that influence the distribution and diversity of lizards, worm-lizards, and snakes (squamate reptiles) in the Amazon Rainforest is essential for biodiversity conservation. However, this task is particularly challenging due to the region's immense size and limited accessibility. In this study, we conducted standardized surveys at 13 sites within the *terra firme* (upland, non-flooded) forests of the Brazilian Amazon. Using pitfall traps and visual encounter surveys, we assessed the abundance, richness, and community composition of squamates. We evaluated the influence of climatic variables (temperature and precipitation), vegetation structure (canopy height and tree density), soil nutrients (base cation concentrations), and proximity to water (Height Above Nearest Drainage, HAND). Our results show that lizard abundance increases with vertical proximity to water, higher soil nutrients, greater canopy height, and higher maximum temperatures in the warmest month, while species richness is driven by temperature seasonality. Community composition is strongly influenced by temperature seasonality, precipitation, and tree density, highlighting the role of climate and habitat structure. Differently, snake abundance decreases with higher precipitation in the wettest month, and no significant patterns emerge for snake richness or composition, likely due to lower detectability and sample size constraints. These findings reveal distinct ecological responses between lizards and snakes, emphasizing the need for conservation strategies that account for these differences, especially amid environmental change in the Amazon Rainforest.

Keywords: Squamata, Community Composition, Environmental Filters, Climate Variability, Vegetation Structure, Soil Nutrients, HAND (Height Above Nearest Drainage), Terra Firme Forest, Amazon Biodiversity.

1. INTRODUCTION

Understanding the patterns of species distribution and the factors responsible for these patterns remain central questions in ecology, with significant implications for biodiversity conservation (Hubbell, 2005; Chase & Myers, 2011). Ecological indices such as species richness and abundance are commonly used to describe the biodiversity of ecosystems (Magurran, 2011; Mittelbach & McGill, 2019). Community composition, defined as the species present and their relative abundances in a given area, also plays a critical role in understanding the ecological dynamics of ecosystems (Vellend, 2010). Characterizing these indices is essential for monitoring biodiversity over time and identifying the environmental and ecological factors that shape biodiversity patterns (Rabosky et al., 2019; Silva et al., 2021). This knowledge is particularly relevant in the Amazon rainforest, where biodiversity is one of the highest in the world (Antonelli et al., 2018; Guayasamin, 2024).

The Amazon Rainforest, which spans nine countries and is the largest tropical rainforest in the world, is renowned for its unparalleled biodiversity, containing nearly 10% of the world's known species (Antonelli et al., 2018; Guayasamin, 2024). This extraordinary diversity results from a combination of ecological, historical, and geographical factors. Its diverse environments, such as upland “terra firme” forests, flooded forests, savannas, and wetlands, provide varied niches supporting distinct biological communities (Fine et al., 2005; Junk et al., 2011; ter Steege et al., 2013; Maximiano et al., 2020). The Amazon’s complex evolutionary history, including the Andean uplift and Pleistocene climatic fluctuations, has further shaped its biodiversity by promoting speciation and adaptation to local conditions (Hoorn et al., 2010). Key environmental factors, such as water availability, soil characteristics, and temperature dynamics, influence the distribution and abundance of Amazonian species.

The Amazon basin harbors remarkable squamate diversity, with approximately 425 species recorded in its Brazilian portion to date (Guedes, Entiauspe-Neto, & Costa, 2023). Species richness continues to increase through new geographical records and descriptions (D'Angiolella et al., 2011; Peloso et al., 2011; Murphy & Jowers, 2013; Ribeiro-Júnior, 2015a, 2015b; Ribeiro-Júnior & Amaral, 2016a, 2016b, 2017; Moura & Jetz, 2021; Costa, Guedes, & Bérnils, 2022; Guedes, Entiauspe-Neto, & Costa, 2023). Ecological studies of squamates (Moraes et al., 2016; de Fraga et al., 2018; Rabosky et al., 2019; Almeida-Corrêa et al., 2020) have largely focused on “terra firme” forests (upland non-flooded areas), utilizing protocols like RAPELD for long-term biodiversity monitoring (Pantoja & de Fraga, 2012; Peixoto et al., 2020; Peixoto et al., 2023; Ganança et al., 2025). These studies are primarily based on visual encounter surveys, but sampling biases and uneven distribution of research effort across the Amazon highlight challenges in understanding squamate distribution patterns (Moura & Jetz, 2021; Ribeiro-Júnior & Amaral, 2016b). Environmental predictors such as distance from streams, canopy openness, and litter depth have been shown to influence squamate community structure, though these predictors often exhibit locality-specific effects, complicating the search for general patterns (Pinto, 2006; de Fraga, Lima, & Magnusson, 2011; Faria, Menin, & Kaefer,

2019; Masseli et al., 2019).

According to community assembly theory, species are distributed in non-random patterns along environmental gradients, where climatic conditions and habitat suitability act as environmental filters (Keddy, 1992; Weiher et al., 2011). These filters select for species adapted to specific conditions, with species richness influenced by niche variability and abundance reflecting species' tolerances and adaptations (Tilman, 1982; Chase & Leibold, 2003). The interplay between structural factors, like vegetation characteristics, and climatic factors, such as temperature and precipitation, is likely to shape the richness, abundance, and composition of squamate communities across Amazonian environments (Yang et al., 2015; de Fraga et al., 2018; Peixoto et al., 2023). Peixoto et al. (2023) found a strong environmental effect and a weak distance effect on the taxonomic and functional composition of lizard communities in the Amazon. However, their study was geographically restricted to a single interfluvial region, limiting the generalization of their findings to the vast Amazon. In this context, the present study aims to investigate the influence of structural and climatic variables on the abundance, richness, and community composition of squamate reptiles (lizards and snakes) in the "terra firme" forests of the Brazilian Amazon at a vastly expanded geographical scale compared to prior studies. Specifically, we ask:

- 1) Which structural and climatic environmental variables most strongly influence species richness?
- 2) How do these variables affect species abundance?
- 3) How do environmental structure and climate shape community composition?

We hypothesize that vegetation-related characteristics—such as tree density, canopy height, soil nutrient levels, and proximity to water—as well as climatic variables like temperature and precipitation, will influence the richness, abundance, and composition of squamate communities. Understanding these relationships is crucial for informing conservation strategies and enhancing our knowledge of the ecological patterns and drivers that shape biodiversity in the Amazon. By elucidating these factors, our study aims to contribute valuable insights toward the preservation of squamate diversity amidst ongoing environmental changes in the region.

2. METHODS

2.1 – Study site

This study was conducted in 13 locations distributed across distinct biogeographic regions (Ribas et al., 2012) of the Brazilian Amazon, selected to fill sampling gaps (Carvalho et al., 2023; Guedes et al., 2018) and encompass diverse environmental conditions (Figure 1). These regions represent a broad spectrum of habitat types and environmental gradients, allowing a comprehensive analysis of factors influencing squamate communities. The surveys were conducted over four years, from 2019 to 2023, with a break in 2020 due to the pandemic. All fieldwork

took place during the drier period (May to December) to standardize sampling conditions. In each location, three 1-km transects (designated A, B, and C) were established in a straight line within the vegetation, with a minimum distance of 1 km between transects to ensure spatial independence.

2.2 – Field Sampling and Specimen Processing

Along each 1-km transect, we installed three Y-shaped pitfall trap arrays at specific intervals: one at the starting point (0 m), one at the midpoint (500 m), and one at the endpoint (1,000 m). Each Y-shaped pitfall trap array consisted of three 10-meter-long arms of drift fence arranged in a Y configuration, converging into four 60-liter buckets—one placed at the central intersection of the fences and one at the end of each arm—to capture ground-dwelling squamate reptiles (Ribeiro-Júnior, Gardner, & Ávila-Pires, 2008). The drift fences acted as barriers that directed moving animals into the buckets, enhancing the effectiveness of the traps. Pitfall traps were operated continuously for nine consecutive nights at each transect, resulting in a total of 1,053 trap-nights across the study sites.

For the visual surveys, a 250-meter section of each 1-km transect was systematically searched to observe species within the vegetation and leaf-litter habitats (Martins & Oliveira, 1998; Scott, Crump, & Zimmerman, 1994). The surveys covered a 20-meter-wide band, extending 10 meters on each side of the transect line. Visual searches were conducted between the 500 m and 750 m marks of each transect by two experienced herpetologists, with separate diurnal and nocturnal sessions. Diurnal surveys took place from 16:00 to 18:00, and nocturnal surveys from 19:00 to 20:20, with each survey lasting between 40 and 80 minutes. Each transect was surveyed six times in total (three diurnal and three nocturnal surveys). In total, the visual surveys resulted in approximately 234 person-hours of field effort.

To minimize interference between sampling methods, the pitfall trap at 500 m and the starting point of the visual survey (500 m) were separated by at least 20 meters. This ensured that one method did not influence the results of the other, maximizing the detection of squamate species across different microhabitats and strata. Additionally, any incidental encounters during transect displacement were recorded, contributing supplementary data on species occurrence across the study areas.

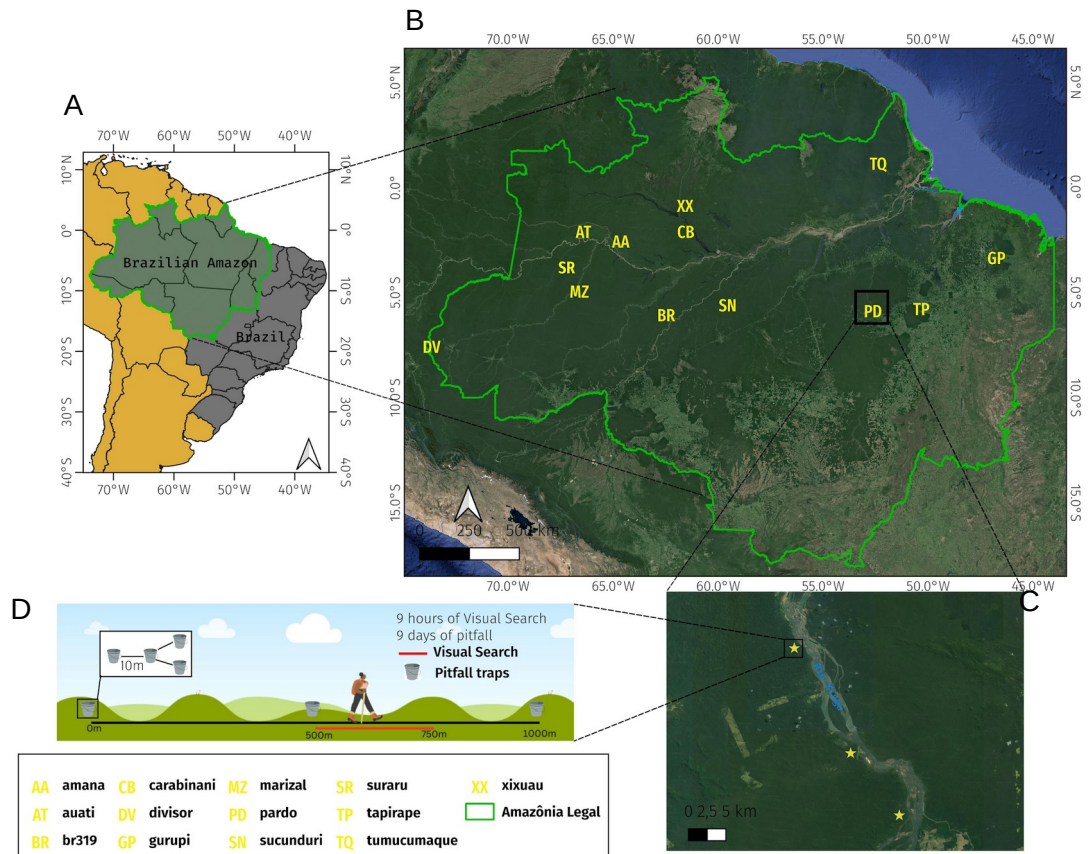


Figure 1 - Sampling points of the ABC expeditions throughout the Brazilian Amazon Forest. Three transects were established in each sampling area. Three pitfall traps were installed along each transect, spaced 500 meters apart. A) Location of the study region within the Amazon basin. B) Location of the sampling areas. C) Location of each transect within the sampling area. D) Schematic drawing of pitfall traps and visual search along the transect.

Species that could not be identified in the field were collected and euthanized via peritoneal injection of 10% lidocaine solution, following ethical guidelines (Pisani, 1973). Specimens were then fixed in 10% formalin for 24 hours before being transferred to 70% ethanol for preservation. Specimens were deposited in the herpetological collections of the Instituto Nacional de Pesquisas da Amazônia (INPA-H) and the Coleção Herpetológica of the Federal University of Santa Catarina (CHUFSC). Taxonomic identification of all species followed the keys provided by Ávila-Pires (1995), Peters and Donoso-Barros (1970), and Vitt et al. (2007) for lizards, and Ferrarezzi and Monteiro (2001), Peters and Orejas-Miranda (1970), and Zaher (1999) for snakes. Species nomenclature was based on The Reptile Database (Uetz, accessed in 2024).

2.3 – Environmental variables

Environmental variables were collected to assess habitat suitability along each location. We employed QGIS software to extract the necessary raster data, enabling precise spatial analysis of environmental conditions at each study site. We initially

gathered 19 bioclimatic variables from WorldClim Version 2 (Fick & Hijmans, 2017) and additional data from other sources, including the Aridity Index (Zomer, Xu, & Trabucco, 2022), global canopy height data (Lang et al., 2023), soil base cation concentrations (Zuquim et al., 2023), and Height Above Nearest Drainage (HAND) (Banon, 2013). We also collected data on elevation and recorded the number of trees in each transect during field surveys. The selection of these variables was based on their ecological relevance to squamate communities and their ability to capture key environmental gradients such as climate, topography, and vegetation structure. We focused on variables known to influence species distribution and community structure in tropical ecosystems.

To avoid collinearity, we performed a correlation analysis to identify and retain variables that were not highly correlated with each other. Variables with correlation coefficients (r) above 0.7 were considered redundant and excluded from further analysis. Specifically, we retained five climatic variables: Mean Diurnal Range (BIO2), Temperature Seasonality (BIO4), Max Temperature of Warmest Month (BIO5), Precipitation of Wettest Month (BIO13), and Precipitation of Coldest Quarter (BIO19). From the other environmental variables, only elevation was discarded due to high collinearity with other topographic features (e.g., HAND). The final selection of 10 variables was used for further analyses.

2.4 - Data Analysis

For the data analysis, each location was treated as an independent sample unit ($N=13$). We confirmed that the environmental variables were not significantly correlated with each other (Supplementary Material; Fig. S1). All analyses were performed using R software (version 4.2.2; R Core Team, 2023), and visualizations were created using the ggplot2 (Wickham, 2016) and cowplot (Wilke, 2020) packages.

To assess the influence of selected environmental variables on the richness and abundance of lizards and snakes, we used generalized linear models (GLMs). Separate models were fitted for richness and abundance as dependent variables. Independent variables included climatic and habitat factors such as temperature seasonality (TempSsn), precipitation of the coldest quarter (PrecpColdQ), aridity index (Aridity), number of trees (n_tree), canopy height (Copa_Height), soil base cation concentrations (Soil_map), maximum temperature of the warmest month (MaxTWarm), mean diurnal temperature range (MD_Range), and height above nearest drainage (HAND). We used either a Poisson distribution (using the glm function from the stats package) or a negative binomial distribution (using the glm.nb function from the MASS package) depending on model fit, with the decision guided by assessment of overdispersion (Venables & Ripley, 2002). Overdispersion was evaluated by comparing the residual deviance to the degrees of freedom; a ratio substantially greater than one indicated overdispersion, prompting the use of the negative binomial distribution. We validated model assumptions using graphical diagnostics, including residual plots from the simulateResiduals function in the DHARMA package (Hartig, 2016). Model selection was based on corrected Akaike

Information Criterion (AICc) values (Burnham & Anderson, 2002) obtained using the dredge function from the MuMIn package (Bartoń, 2023). Variables were retained in the models if their importance factor was greater than 0.6 on a 0 to 1 scale, based on their frequency of occurrence in the best-fitting models (Burnham & Anderson, 2002; Almeida et al., 2023).

To investigate how environmental variables influenced the composition of lizard and snake communities, we performed a Permutational Analysis of Variance (PERMANOVA) (Clarke, 1993) using the `adonis2` function from the `vegan` package in R (Oksanen et al., 2020), with 99,999 permutations. This non-parametric multivariate analysis allowed us to assess the proportion of variation in species composition that could be explained by environmental factors. We tested for spatial autocorrelation in species richness and abundance using Moran's I statistic, calculated with the `Moran.I` function from the `ape` package (Paradis & Schliep, 2019). The results were non-significant for both richness (Moran's I = 0.033, $p = 0.32$) and abundance (Moran's I = 0.076, $p = 0.47$), suggesting no spatial dependence in the distribution of these variables.

We analyzed species composition using two approaches. First, we used the Bray-Curtis dissimilarity index to evaluate the effects of environmental variables on species abundance data. The Bray-Curtis index is sensitive to abundances and emphasizes differences in species composition due to changes in abundance (Clarke & Warwick, 2001). Second, to reduce the influence of species abundances and focus on species occurrence, we used the Jaccard similarity index, which is based on species presence-absence data (Gotelli & Ellison, 2013).

We also performed redundancy analysis (RDA) using the `rda` function from the `vegan` package (Oksanen et al., 2020) to visualize ordinations and assess relationships between environmental variables and community composition. RDA allowed us to explore the linear relationships between the species data and environmental predictors, facilitating interpretation of the multivariate patterns in community composition.

3.RESULTS

3.1 - Community composition

A total of 1169 individuals belonging to 109 species and 17 families were recorded. Lizards accounted for nine families: Anolidae, Hoplocercidae, Teiidae, Gymnophthalmidae, Tropiduridae, Alopoglossidae, Sphaerodactylidae, Scincidae, Phyllodactylidae, and Leiosauridae (*sensu* Zheng & Wiens, 2016). The most frequently sampled lizard species were *Kentropyx pelviceps* (130 individuals, 11.5% of all individuals), *Chatogekko amazonicus* (129 individuals, 11.4%), and *Loxopholis guianensis* (81 individuals, 7.1%).

Snakes were represented by eight families: Aniliidae, Boidae, Colubridae, Elapidae, Leptotyphlopidae, Typhlopidae, and Viperidae. The most commonly recorded snake species were *Bothrops atrox* (14 individuals, 1.2%), *Imantodes cenchoa* (12 individuals, 1%), and *Epicrates cenchria* (5 individuals, 0.4%).

3.2 - Effects on abundance

Lizard abundance was positively associated with proximity to water sources, higher soil nutrient levels, increased canopy height and maximum temperature in the warmest month. (Fig. 2A). Snake abundance, on the other hand, demonstrated a negative relationship with precipitation during the wettest month (Fig. 2B).

3.3 - Effects on richness

Lizard richness exhibited a positive association with temperature seasonality, while snake richness did not show significant relationships with any of the tested environmental variables (Fig. 2C,D).

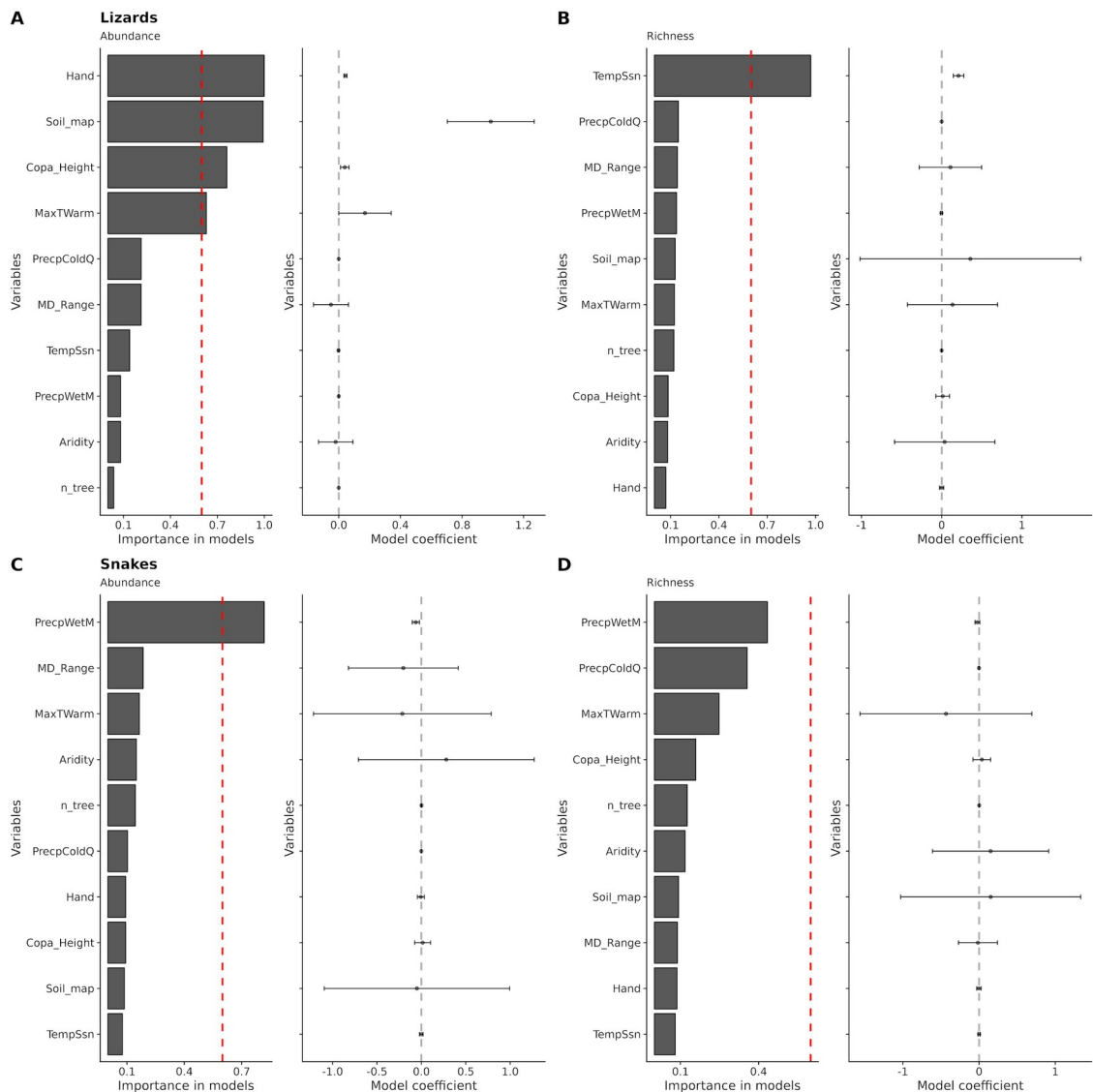


Figure 2: Relative importance of each variable in the best-fitting models for a) Lizards abundance b) Snake abundance c) Lizards Richness d) Snakes Richness. The vertical red lines indicate the importance threshold (importance > 0.6). Positive and negative effects of variables are indicated by model coefficients. Variables tested: Temperature Seasonality

(TempSsn), Precipitation of the Coldest Quarter (PrecpColdQ), Aridity Index (Aridity), Number of Trees (n_tree), Precipitation of the Wettest Month (PrecpWetM), Max Temperature of the Warmest Month (MaxTWarm), Mean Diurnal Range (MD_Range), Canopy Heights (Copa_Height), Height Above Nearest Drainage (Hand), and Soil Sum Base of Cations (Soil_map).

3.4 - Effects on composition

The composition of lizard communities was significantly influenced by environmental variables. Permutational Analysis of Variance (PERMANOVA) indicated that Precipitation of the Wettest Month ($F = 2.329$, $p=0.009$) (PrecpWetM), Precipitation of the Coldest Quarter ($F = 2.313$, $p=0.016$) (PrecpColdQ), Temperature Seasonality ($F = 2.429$, $p=0.006$) (TempSsn) and Number of Trees ($F = 1.829$, $p=0.049$) (n_tree) had significant effects on lizard species composition when abundance data were considered (Table S4). Redundancy Analysis (RDA) further illustrated these relationships, with the first two axes explaining 21.99% of the variation in community composition (Fig. 3A). The directional vectors in the RDA plot showed that variations in precipitation, temperature seasonality and number of trees were associated with changes in lizard species abundances across the surveyed locations.

When species presence-absence data were analyzed, the Aridity Index (Aridity) emerged as the significant environmental variable influencing lizard community composition (PERMANOVA: $F = 2.774$, $p = 0.001$; Table S4). The RDA based on presence-absence data demonstrated that aridity was associated with shifts in the occurrence of lizard species among sites (Fig. 3C). The ordination plot indicated that areas with different levels of aridity harbored distinct lizard assemblages.

In contrast, snake community composition did not show significant associations with any of the tested environmental variables, regardless of whether abundance or presence-absence data were used (PERMANOVA: all $p > 0.05$; Table S4). The RDA plots for snakes displayed no strong gradients or clustering patterns related to the measured environmental factors (Fig. 3B,D). This suggests that snake species composition remained relatively consistent across the environmental gradients studied, with no detectable changes in species abundance or presence linked to the environmental variables assessed.

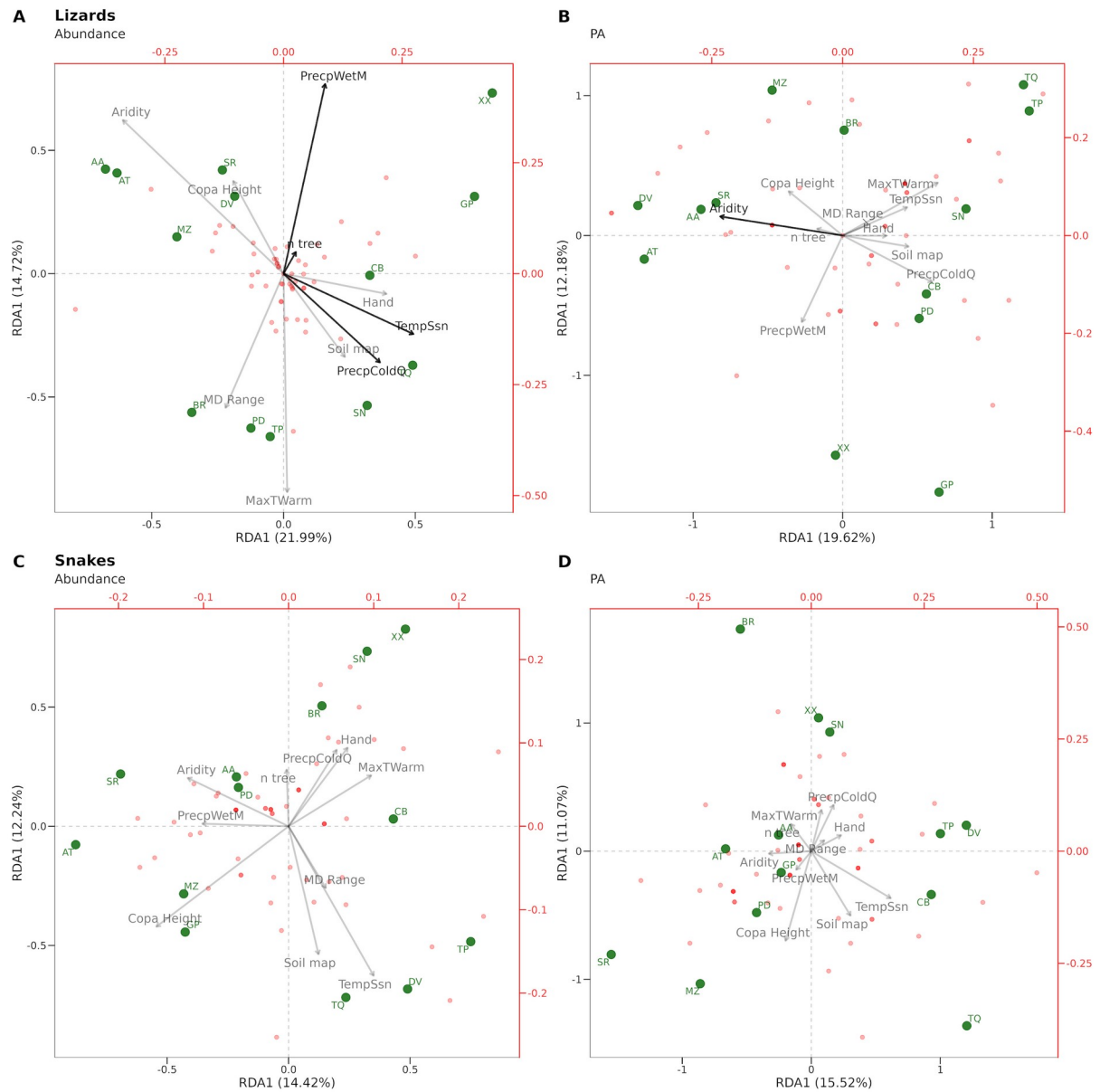


Figure 3: Redundancy Analysis (RDA) ordination plots illustrating the relationships between environmental variables and community composition. (A) Lizard community composition based on abundance data; (B) Lizard community composition based on presence-absence data. (C) Snake community composition based on abundance data; ; (D) Snake community composition based on presence-absence data. Arrows represent significant environmental variables influencing community composition, with the length and direction indicating the strength and nature of the relationships. Transparency in arrows indicates variables not selected based on statistical significance ($p > 0.05$). Survey locations are represented by dots, and their distribution reflects similarities and differences in species composition in relation to environmental gradients.

4. DISCUSSION

Our study across the Amazon Forest revealed strong environmental influences on squamate communities, particularly for lizards. Environmental gradients, including temperature seasonality, precipitation patterns, and habitat structure, emerged as key drivers of community organization (Diele-Viegas & Rocha, 2018; Shah et al., 2017). While lizard assemblages showed clear responses to these gradients, snake patterns were less evident, likely due to sampling limitations inherent to their cryptic nature (MacKenzie & Kendall, 2002; de Fraga et al., 2014). The complex interplay between climatic variables and habitat characteristics suggests that maintaining environmental heterogeneity is crucial for preserving squamate diversity in Amazonian forests. These findings contribute to our understanding of how environmental factors shape tropical forest communities and have important implications for predicting responses to environmental change (Guayasamin et al., 2024).

The composition of squamate communities reflected strong environmental filtering across the Amazon Forest. Temperature seasonality emerged as a primary driver of community structure, with distinct assemblages occurring along thermal gradients. Areas with greater temperature variation supported unique species combinations, challenging traditional expectations about tropical species' narrow thermal tolerances (Diele-Viegas & Rocha, 2018; Shah et al., 2017). For snakes, community patterns were less clear, possibly due to their cryptic nature and lower detection rates (MacKenzie & Kendall, 2002; de Fraga et al., 2014). Precipitation shaped community composition differently across taxa - while excessive rainfall during wet periods altered snake assemblages through reduced activity periods (Lillywhite, 2014; Turci et al., 2021), moderate precipitation was associated with distinct lizard assemblages (de Fraga et al., 2018). The limited snake observations (160 individuals across 13 locations) suggest cautious interpretation of these patterns (Mazerolle et al., 2007).

Habitat complexity drove distinct patterns in squamate community composition. Areas with taller canopies and higher tree density supported unique lizard assemblages (Vitt et al., 2007; Faria et al., 2019), suggesting strong environmental filtering based on vertical habitat structure. While snake assemblage patterns showed no significant association with habitat structure, this likely reflects their diverse habitat use strategies, including arboreal and fossorial habits, rather than absence of habitat filtering (Kéry, 2002; de Fraga et al., 2014). Soil nutrient gradients further shaped community composition, particularly for lizards, through their influence on vegetation structure and resource availability (Zuquim et al., 2023; Pinto, 2006).

Water body proximity created distinct gradients in community composition, particularly evident in lizard assemblages (Peixoto et al., 2020; Faria et al., 2019). These spatial patterns suggest that moisture gradients act as environmental filters, creating distinct communities at different distances from water. While snake assemblage composition showed no clear spatial patterns, methodological limitations

suggest the need for targeted studies to better understand their spatial organization (de Fraga et al., 2014).

Our understanding of community patterns must be viewed through the lens of sampling limitations. While visual surveys and pitfall traps effectively captured lizard diversity, snake detection was notably lower. This disparity suggests the need for extended sampling periods and longer transect surveys to better account for snake movement patterns and activity cycles (de Fraga et al., 2014; MacKenzie & Kendall, 2002). Future studies might benefit from employing multiple sampling techniques across seasons and expanding spatial coverage to better capture the full spectrum of squamate diversity.

The strong environmental filtering we observed has crucial implications for conservation planning. As climate change and habitat modification alter temperature seasonality and precipitation patterns, squamate communities may undergo significant restructuring. Areas with high environmental heterogeneity could serve as refugia, maintaining diverse assemblages through the provision of various microhabitats and thermal environments (Diele-Viegas & Rocha, 2018). The distinct community responses to water proximity emphasize the importance of preserving riparian corridors and maintaining landscape connectivity.

Several key research priorities emerge from our findings. Long-term monitoring is essential to understand temporal dynamics in community composition, particularly given increasing climate variability. More extensive transect sampling and prolonged survey periods could reveal patterns in snake communities obscured in our current analysis. Additionally, investigating species' functional traits and their relationship with environmental gradients could provide mechanistic insights into community assembly processes (Peixoto et al., 2023). Understanding these aspects will be crucial for predicting and managing community responses to environmental change.

5.CONCLUSION

Environmental gradients strongly influence squamate community organization in the Amazon Forest, operating through multiple filtering mechanisms. Temperature seasonality, habitat complexity, and water proximity emerged as key drivers shaping community composition, particularly for lizards. While methodological constraints limited our understanding of snake assemblages, our findings reveal how environmental heterogeneity maintains diverse squamate communities across Amazonian landscapes. The distinct responses to environmental gradients suggest that preserving habitat heterogeneity, especially around water bodies and areas with complex vegetation structure, will be crucial for squamate conservation. As climate change and habitat modification continue to affect the Amazon Forest, understanding these environmental filtering processes becomes increasingly important for predicting and managing community responses. Future research employing extended sampling periods and broader spatial coverage will be essential to fully comprehend the dynamics of these diverse tropical communities, particularly for cryptic taxa like snakes.

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7. SUPPLEMENTARY MATERIAL

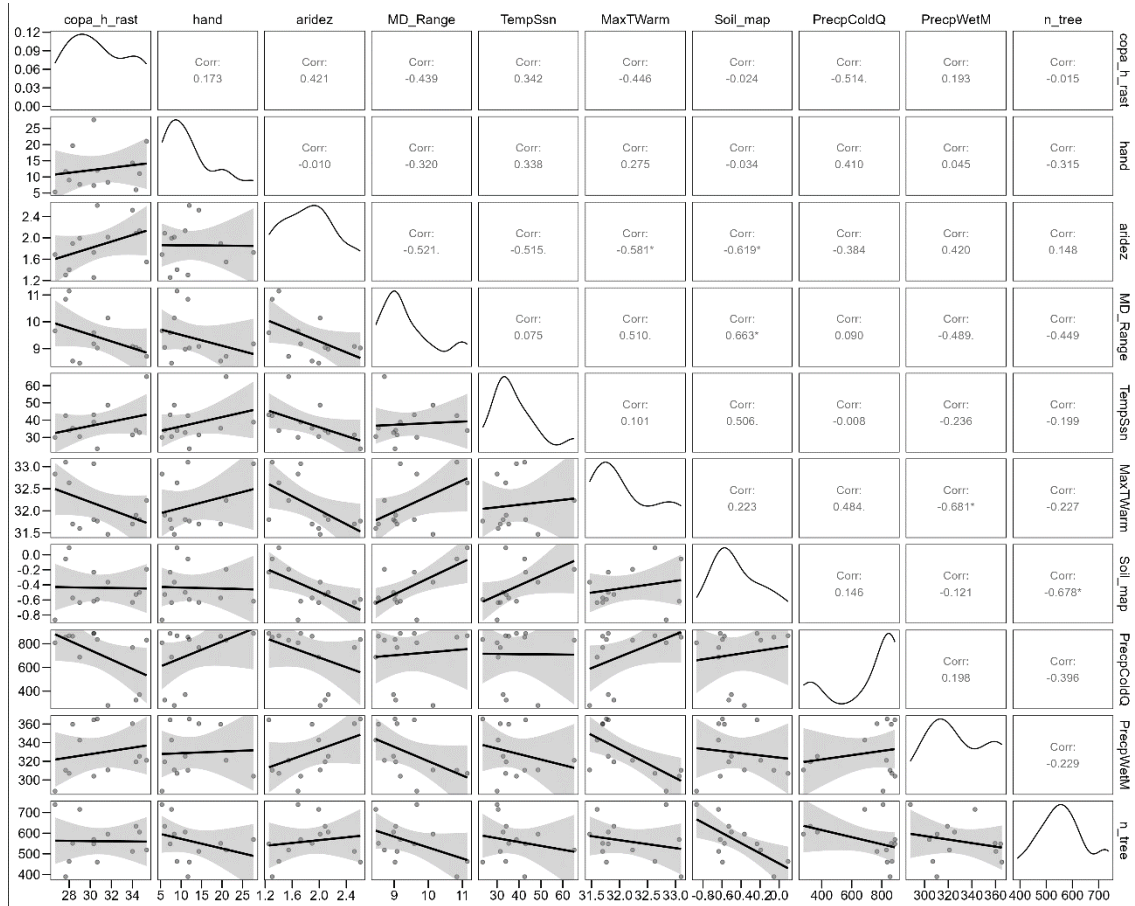


Figure S1: Correlation panel between predictor variables. The black line shows the trend in the relationship. (Temperature Seasonality = TempSsn, Precipitation of the Coldest Quarter = PrecpColdQ, Aridity Index = Aridez, Number of Trees = n_tree, Precipitation of the Wettest Month = PrecpWetM, Max Temperature of the Warmest Month = MaxTWarm, Mean Diurnal Range = MD_Range, Canopy Heights = Copa_Height, Height Above Nearest Drainage = Hand, and Soil Sum Base of Cations = Soil_map).

Table S2: Results of the best models ($\Delta AICc < 2$) for the relationship between lizards and snakes species richness/abundance and environmental variables selected. We considered the effect of each variable and double interactions. Models are ranked from best to worst according to model $\Delta AICc$. K the numbers of estimated parameters for each model. (1 = Aridity, 2 = Copa_Height, 3 = Hand, 4 = MaxTWarm, 5 = MD_Range, 6 = n_tree, 7 = PrecpColdQ, 8 = PrecpWetM, 9 = Soil_map and 10= TempSsn).

Reponse	Model	$\Delta AICc$	AICc	K	wAICc
Lizard (Abundance)	2+3+4+9	0.00	135.82	5	0.36
Lizard (Richness)	10	0.00	58.91	3	0.27
Snake (Abundance)	8	0.00	63.31	3	0.18
	5+8	1.51	64.82	4	0.09
	1+8	1.81	65.13	4	0.07
	4+8	1.83	65.14	4	0.07
Snake (Richness)	7	0.00	55.93	3	0.13
	4+8	0.18	56.11	4	0.12
	(Null)	1.16	57.10	2	0.07
	8	1.91	58.97	3	0.05

Table S3: PERMANOVA result for the influence of environmental variables (Temperature Seasonality = TempSsn, Precipitation of the Coldest Quarter = PrecpColdQ, Aridity Index = Aridity, Number of Trees = n_tree, Precipitation of the Wettest Month = PrecpWetM, Max Temperature of the Warmest Month = MaxTWarm, Mean Diurnal Range = MD_Range, Canopy Heights = Copa_Height, Height Above Nearest Drainage = Hand, and Soil Sum Base of Cations = Soil_map) on the composition of lizards and snakes. The variables were ordered in the model according to the R² value calculated individually.

Response	Explicativa	Df	Sum Of Sqs	R ²	Pseudo F	p value	Individual R ²
Lizard (Abundance)	TempSsn	1	0.557	0.139	2.492	0.006	0.139
	PrecpColdQ	1	0.517	0.129	2.313	0.016	0.128
	Aridity	1	0.292	0.073	1.308	0.225	0.133
	n_tree	1	0.408	0.102	1.829	0.049	0.112
	PrecpWetM	1	0.520	0.130	2.329	0.009	0.111
	MaxTWarm	1	0.166	0.042	0.745	0.765	0.107
	MD_Range	1	0.273	0.068	1.224	0.281	0.099
	Copa_Height	1	0.177	0.044	0.790	0.711	0.094
	Hand	1	0.388	0.097	1.736	0.065	0.091
	Soil_map	1	0.258	0.064	1.154	0.340	0.085
	Residual	2	0.447	0.112			
	Total	12	4.003	1.000			
Lizard (PA)	Aridity	1	0.656	0.182	2.774	0.001	0.181
	MaxTWarm	1	0.340	0.094	1.439	0.130	0.136
	PrecpColdQ	1	0.355	0.098	1.501	0.112	0.124
	PrecpWetM	1	0.229	0.063	0.967	0.514	0.130
	Copa_Height	1	0.282	0.078	1.191	0.286	0.115
	TempSsn	1	0.216	0.060	0.915	0.579	0.095
	Soil_map	1	0.277	0.077	1.172	0.304	0.105
	MD_Range	1	0.303	0.084	1.282	0.216	0.100
	Hand	1	0.280	0.077	1.186	0.289	0.083
	n_tree	1	0.196	0.054	0.832	0.691	0.079
	Residual	2	0.473	0.131			
	Total	12	3.610	1.000			

Response	Explicativa	Df	Sum Of Sqs	R ²	Pseudo F	p value	Individual
Snake (Abundance)	Copa_Height	1	0.452	0.107	1.105	0.359	0.107
	TempSsn	1	0.461	0.109	1.128	0.329	0.096
	Hand	1	0.436	0.103	1.068	0.401	0.093
	Soil_map	1	0.324	0.077	0.793	0.762	0.092
	n_tree	1	0.283	0.067	0.694	0.866	0.073
	Aridity	1	0.229	0.054	0.561	0.957	0.075
	PrecpWetM	1	0.272	0.065	0.666	0.892	0.073
	MD_Range	1	0.334	0.079	0.817	0.720	0.065
	MaxTWarm	1	0.246	0.058	0.602	0.936	0.061
	PrecpColdQ	1	0.342	0.081	0.837	0.696	0.053

Response	Explicativa	Df	Sum Of Sqs	R ²	Pseudo F	p value	Individual
	Residual	2	0.817	0.194			
	Total	12	4.199	1.000			
Snake (PA)	TempSsn	1	0.451	0.096	1.061	0.386	0.096
	Hand	1	0.453	0.096	1.066	0.383	0.089
	Soil_map	1	0.321	0.068	0.755	0.875	0.089
	Copa_Height	1	0.512	0.109	1.204	0.206	0.089
	PrecpWetM	1	0.353	0.075	0.830	0.767	0.080
	Aridity	1	0.341	0.072	0.804	0.818	0.078
	MD_Range	1	0.452	0.096	1.063	0.386	0.070
	MaxTWarm	1	0.239	0.051	0.564	0.988	0.067
	n_tree	1	0.318	0.068	0.748	0.882	0.066
	PrecpColdQ	1	0.396	0.084	0.932	0.601	0.063
	Residual	2	0.850	0.181			
	Total	12	4.691	1.000			

Table S3: Eigenvalues and variance explained for the first two axes in the RDA analysis.

Response	Explanatory	RDA1	RDA2
Lizard (Abundance)	Copa_Height	-0.191	0.376
	Hand	0.391	-0.082
	Aridity	-0.610	0.623
	MD_Range	-0.220	-0.544
	TempSsn	0.493	-0.245
	MaxTWarm	-0.014	-0.886
	Soil_map	0.233	-0.338
	PrecpColdQ	0.366	-0.360
	PrecpWetM	0.158	0.769
	n_tree	0.047	0.088
	Eigenvalue	0.149	0.099
	Proportion Explained	21.993	14.718
	Cumulative Proportion	21.993	36.710
Lizard (PA)	Copa_Height	-0.361	-0.316
	Hand	0.293	-0.002
	Aridity	-0.819	0.136
	MD_Range	0.173	0.079
	TempSsn	0.432	0.202
	MaxTWarm	0.637	0.387
	Soil_map	0.441	-0.079
	PrecpColdQ	0.599	-0.334
	PrecpWetM	-0.273	-0.619
	n_tree	-0.171	0.048
	Eigenvalue	1.690	1.049
	Proportion Explained	19.618	12.177
	Cumulative Proportion	19.618	31.795

Response	Explanatory	RDA1	RDA2
Snake (Abundance)	Copa_Height	-0.544	-0.421
	Hand	0.243	0.330
	Aridity	-0.415	0.203
	MD_Range	0.153	-0.259
	TempSsn	0.350	-0.627
	MaxTWarm	0.340	0.214
	Soil_map	0.123	-0.537
	PrecpColdQ	0.198	0.321
	PrecpWetM	-0.355	0.011
	n_tree	-0.008	0.238
	Eigenvalue	0.115	0.098
	Proportion Explained	14.421	12.243
	Cumulative Proportion	14.421	26.664

Response	Explanatory	RDA1	RDA2
Snake (PA)	Copa_Height	-0.199	-0.699
	Hand	0.231	0.125
	Aridity	-0.329	-0.019
	MD_Range	0.101	0.085
	TempSsn	0.616	-0.367
	MaxTWarm	0.079	0.322
	Soil_map	0.304	-0.503
	PrecpColdQ	0.173	0.361
	PrecpWetM	-0.117	-0.145
	n_tree	-0.159	0.212
	Eigenvalue	1.041	0.742
	Proportion Explained	15.524	11.071
	Cumulative Proportion	15.524	26.595

Table S4: Species list of lizards and snakes and localities (AA = Amanã; AT = Auati-Paraná; ; BR = BR319; CB = Rio Carabinani; DV = Serra do Divisor; GP = Gurupi; MZ = Marizal; PD = Serra do Pardo; SN = Rio Sucunduri; SR = Lago Suraru; TQ = Tumucumaque; TP = Tapirapé; XX = Xixau).

Family	Species	Localities
Alopoglossidae	<i>Alopoglossus angulatus</i>	MZ, TQ, DV, PD, AA, TP
Alopoglossidae	<i>Alopoglossus atriventris</i>	DV, MZ, AT, BR
Alopoglossidae	<i>Alopoglossus brevifrontalis</i>	DV, MZ, TP, SR
Alopoglossidae	<i>Alopoglossus buckleyi</i>	AT, SR
Alopoglossidae	<i>Alopoglossus theodoruse</i>	TQ
Anolidae	<i>Anolis chrysolepis</i>	TQ
Anolidae	<i>Anolis fuscoauratus</i>	DV, GP, PD, SN, AT, TP, TQ, BR, MZ, XX
Anolidae	<i>Anolis ortonii</i>	DV
Anolidae	<i>Anolis planiceps</i>	XX
Anolidae	<i>Anolis punctatus</i>	MZ, AT, GP, DV, PD, XX
Anolidae	<i>Anolis scypheus</i>	AT, AA
Anolidae	<i>Anolis tandai</i>	MZ, SR, DV, SN, TQ
Anolidae	<i>Anolis trachyderma</i>	DV
Anolidae	<i>Anolis transversalis</i>	AA, DV, AT, SR
Gymnophthalmidae	<i>Amapasaurus tetradactylus</i>	TQ
Gymnophthalmidae	<i>Arthrosaura kockii</i>	TQ, TP
Gymnophthalmidae	<i>Arthrosaura reticulata</i>	XX, CB, AT, MZ, GP, TQ, SR
Gymnophthalmidae	<i>Bachia flavescens</i>	XX
Gymnophthalmidae	<i>Cercosaura anordosquama</i>	SN
Gymnophthalmidae	<i>Cercosaura argulus</i>	PD, GP, TP, SN
Gymnophthalmidae	<i>Cercosaura bassleri</i>	BR, SR
Gymnophthalmidae	<i>Cercosaura ocellata</i>	TP, BR, CB
Gymnophthalmidae	<i>Cercosaura olivacea</i>	GP
Gymnophthalmidae	<i>Cercosaura oshaughnessyi</i>	DV
Gymnophthalmidae	<i>Chatogekko amazonicus</i>	TP
Gymnophthalmidae	<i>Iphisa elegans</i>	MZ, TQ, CB, SR, AA, SN
Gymnophthalmidae	<i>Iphisa soinii</i>	DV
Gymnophthalmidae	<i>Loxopholis guianense</i>	TQ, TP
Gymnophthalmidae	<i>Loxopholis osvaldoi</i>	BR, SN
Gymnophthalmidae	<i>Loxopholis percarinatum</i>	GP, PD, XX, TP, CB
Gymnophthalmidae	<i>Loxopholis snethlageae</i>	MZ, AA, AT, SR
Gymnophthalmidae	<i>Neusticurus bicarinatus</i>	TP
Gymnophthalmidae	<i>Tretioscincus agilis</i>	TP
Hoplocercidae	<i>Enyalioides laticeps</i>	AA, AT, SR, DV
Leiosauridae	<i>Enyalius leechii</i>	SN
Phyllodactylidae	<i>Thecadactylus rapicauda</i>	GP, PD, TQ
Scincidae	<i>Copeoglossum nigropunctatum</i>	BR, GP, TP, MZ, PD, SN, TQ, AA
Scincidae	<i>Varzea bistrata</i>	CB
Sphaerodactylidae	<i>Chatogekko amazonicus</i>	MZ, PD, SN, TP, TQ, CB, BR
Sphaerodactylidae	<i>Coleodactylus meridionalis</i>	GP
Sphaerodactylidae	<i>Gonatodes annularis</i>	TQ
Sphaerodactylidae	<i>Gonatodes eladioi</i>	PD
Sphaerodactylidae	<i>Gonatodes hasemani</i>	BR, DV
Sphaerodactylidae	<i>Gonatodes humeralis</i>	CB, GP, MZ, PD, XX, DV, SN, TP, SR
Sphaerodactylidae	<i>Pseudogonatodes guianensis</i>	XX, AT, TQ, SN, DV, CB
Teiidae	<i>Ameiva ameiva</i>	GP, SN, AA, CB, TQ, MZ, TP
Teiidae	<i>Crocodylus amazonicus</i>	CB, PD
Teiidae	<i>Kentropyx altamazonica</i>	CB

Teiidae	<i>Kentropyx calcarata</i>	SN, GP, TQ, XX
Teiidae	<i>Kentropyx pelviceps</i>	BR, CB, MZ, TP, AT, DV, AA, PD, SR
Tropiduridae	<i>Plica plica</i>	SR, TP, BR, SN, TQ
Tropiduridae	<i>Plica umbra</i>	AA, GP, SN, TQ, MZ, PD, TP, CB, DV
Tropiduridae	<i>Uranoscodon superciliosus</i>	XX, AT, TP, AA
Aniliidae	<i>Anilius scytale</i>	SR
Boidae	<i>Boa constrictor</i>	TP, DV
Boidae	<i>Corallus batesii</i>	AT, SR
Boidae	<i>Epicrates cenchria</i>	DV, SN, TP, TQ, CB
Colubridae	<i>Adelphostigma quadriocellata</i>	BR
Colubridae	<i>Apostolepis nigrolineata</i>	AA
Colubridae	<i>Atractus badius</i>	TQ
Colubridae	<i>Atractus boimirim</i>	SN
Colubridae	<i>Atractus caxiuna</i>	SN
Colubridae	<i>Atractus major</i>	XX
Colubridae	<i>Atractus poeppigi</i>	CB
Colubridae	<i>Atractus snethlageae</i>	BR, SR
Colubridae	<i>Atractus torquatus</i>	CB, SR
Colubridae	<i>Chironius exoletus</i>	PD
Colubridae	<i>Chironius fuscus</i>	CB, XX
Colubridae	<i>Chironius multiventris</i>	MZ, AT
Colubridae	<i>Chlorosoma viridissimum</i>	XX
Colubridae	<i>Clelia clelia</i>	BR, DV
Colubridae	<i>Dendrophidion dendrophis</i>	AT, TQ
Colubridae	<i>Dipsas catesbyi</i>	SN, XX, PD
Colubridae	<i>Dipsas mikanii</i>	GP
Colubridae	<i>Drepanoides anomalus</i>	BR, MZ, PD, SR
Colubridae	<i>Drymarchon corais</i>	SR
Colubridae	<i>Erythrolamprus aesculapii</i>	AA
Colubridae	<i>Erythrolamprus oligolepis</i>	GP, SN, SR
Colubridae	<i>Erythrolamprus reginae</i>	MZ
Colubridae	<i>Erythrolamprus typhlus</i>	DV, GP, AA, BR
Colubridae	<i>Helicops angulatus</i>	BR
Colubridae	<i>Hydrops martii</i>	AT
Colubridae	<i>Imantodes cenchoa</i>	CB, TQ, TP, GP, PD, SR, AA, DV, MZ
Colubridae	<i>Leptodeira annulata</i>	TQ, MZ
Colubridae	<i>Oxybelis aenus</i>	CB
Colubridae	<i>Oxybelis fulgidus</i>	AT, PD
Colubridae	<i>Oxyrhopus melanogenys</i>	DV, GP
Colubridae	<i>Oxyrhopus occipitalis</i>	BR, SN, AA
Colubridae	<i>Oxyrhopus petolarius</i>	DV
Colubridae	<i>Rhinobothryum lentiginosum</i>	CB
Colubridae	<i>Siphlophis cervinus</i>	TQ, CB
Colubridae	<i>Siphlophis compressus</i>	SN, TP, MZ, XX
Colubridae	<i>Spilotes pullatus</i>	TP, DV, TQ
Colubridae	<i>Taeniophalus brevirostris</i>	SR
Colubridae	<i>Xenodon rabdocephalus</i>	AA
Colubridae	<i>Xenopholis scalaris</i>	AA, SR
Colubridae	<i>Xenoxybelis argenteus</i>	PD
Elapidae	<i>Micrurus lemniscatus</i>	GP
Elapidae	<i>Micrurus hemprichii</i>	AT, MZ
Elapidae	<i>Micrurus langsdorffi</i>	BR
Elapidae	<i>Micrurus paraensis</i>	AA
Elapidae	<i>Micrurus remotus</i>	SR, MZ
Leptotyphlopidae	<i>Epictia albifrons</i>	TQ
Typhlopidae	<i>Amerotyphlops minuisquamus</i>	SR

Typhlopidae	<i>Amerotyphlops reticulatus</i>	PD
Viperidae	<i>Bothrops atrox</i>	PD, AA, BR, TQ, TP, CB, DV, MZ, SN, XX
Viperidae	<i>Bothrops bilineatus</i>	PD, TQ
Viperidae	<i>Bothrops brazili</i>	DV
Viperidae	<i>Lachesis muta</i>	PD

5. CAPÍTULO 3 - Sampling method effects on taxonomic and functional diversity patterns of lizards and snakes in the Brazilian Amazon

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ABSTRACT PAGE

Sampling method effectiveness in biodiversity surveys can significantly influence our understanding of community patterns, particularly in megadiverse tropical forests. However, how different sampling methods affect our perception of taxonomic versus functional diversity remains poorly understood. We evaluated how three sampling methods (pitfall traps, active search, and occasional encounters) influence estimates of taxonomic and functional diversity of lizards and snakes across 13 locations in the Brazilian Amazon. We found contrasting effectiveness patterns between lizards and snakes, with significant implications for biodiversity assessments. For lizards, pitfall traps were most effective, capturing 45 species (578 individuals), while active search and occasional encounters recorded 33 and 30 species, respectively. Conversely, for snakes, occasional encounters were most efficient, recording 43 species (79 individuals), followed by active search (23 species) and pitfall traps (11 species). While sampling methods significantly influenced taxonomic diversity and composition for both groups, they showed no significant effect on functional diversity patterns, possibly reflecting functional redundancy in tropical squamate communities or limitations of our categorical trait approach. Species accumulation curves and compositional analyses revealed strong method-specific biases in lizards and snakes species detection, highlighting the importance of combining methods for comprehensive surveys. Our results suggest that while multiple sampling methods are essential for complete taxonomic inventories, individual methods might adequately capture broad functional diversity patterns. These findings provide important insights for optimizing sampling protocols in tropical forests and underscore the need to consider both taxonomic and functional components when designing biodiversity surveys.

Keywords: Squamata, Sampling Methods, Taxonomic Diversity, Functional Diversity, Pitfall Traps, Active Search, Occasional Encounters, Community Composition, Methodological Bias, Amazon.

1. INTRODUCTION

Accurate assessment of biodiversity is fundamental for understanding community assembly, ecosystem functioning, and for informing conservation strategies. Tropical regions, and the Brazilian Amazon in particular, harbor an exceptionally high diversity of reptiles with many new species continuing to be discovered (e.g. Antonelli et al., 2018; Guayasamin, 2024). Despite this impressive diversity, the conservation status of many reptile species remains poorly understood (Böhm et al., 2013; Rodrigues, M.T., 2005; Li et al., 2024). In this context, obtaining reliable estimates of species composition, abundance, and functional roles is of critical importance for both ecological research and conservation planning (Scott et al., 1992; Snodgrass et al., 2000, Azevedo et al., 2024).

Field studies of reptiles face unique challenges, not least of which is the selection of appropriate sampling methods. Reptiles exhibit diverse life histories and microhabitat preferences—with many terrestrial or semi-arboreal lizards being conspicuous and readily observed, in contrast to snakes that are often secretive, cryptic, and rare (Freitas et al., 2017; Peixoto et al., 2019). Moreover, reptiles contribute substantially to ecosystem processes: they serve as major predators, dispersers, and engineers of habitat via their interactions with plants, prey, and microclimatic conditions (Pianka, 1973; Jones et al., 1994, Miranda, 2017). Because the outcomes of ecological studies are highly dependent on the chosen sampling technique, it is essential to consider not only capture rates but also the repeatability and bias (Gibbons & Semlitsch, 1981; Gotelli & Colwell, 2001). For example, while visual encounter surveys (VES) and transect methods can cover large areas at low cost and are effective for species that are active and visible, they may underestimate the diversity of elusive or cryptic species (Crump & Scott, 1994; Doan, 2003). Conversely, total removal plots or passive trapping techniques (e.g., pitfall traps, cover boards, and drift fences) are often more effective for secretive, fossorial, or small-bodied reptiles, yet they require extensive time, effort, and financial investment (Gardner et al., 2008; Fraga et al., 2014).

Standardized plot and transect censuses are popular because they quantify abundance, density, and species richness in a repeatable manner across space and time (Marsh & Haywood, 2010, Dodd, 2016). Techniques such as RAPELD, which spatially standardize transects along altitudinal contours to minimize habitat heterogeneity, have dramatically improved comparisons among sites in the Amazon (Magnusson et al., 2005; Magnusson et al., 2013). Yet challenges remain in fully capturing reptile diversity: even with standardized sampling, many inventories remain incomplete due to low detectability or uneven capture probabilities among taxa (Gotelli & Colwell, 2001; Dodd et al., 2016).

Ultimately, the choice of sampling method and the associated statistical tools can affect estimates of both taxonomic and functional diversity. While taxonomic diversity (expressed as species richness, heterogeneity, and evenness) is relatively straightforward to measure, integrating data into indices that reflect functional diversity (i.e., the range of ecological traits present in the community) offers additional insights into ecosystem functioning and resilience (Gotelli & Graves, 1996; Magurran, 2013). Notably, several studies suggest that, despite differences in raw species counts across sampling methods, the overall functional trait space captured by different techniques may be notably similar—

potentially reflecting a degree of functional redundancy in these hyperdiverse tropical communities (Hubbell, 2001).

Recent inventories from diverse sites in the Amazon underscore the value of an integrated methodological approach. For instance, Peixoto et al. (2019) documented the geographic distribution of lizards along the road BR-319 in the Purus-Madeira interfluvium, while inventories in the Reserva Extrativista do Rio Gregório (Pantoja & Fraga et al., 2012) combined pitfall traps, active searches, and opportunistic encounters to yield a comprehensive herpetofaunal list. Similarly, mesoscale studies by de Fraga (2011) illustrate that local habitat gradients, such as those occurring in riparian corridors, can structure snake assemblages in ways that might be masked by large-scale surveys.

In this study, we evaluate how three distinct sampling methods—pitfall traps with drift fences, active visual searches, and occasional encounters—influence estimates of both taxonomic and functional diversity of lizards and snakes across 13 locations in the Brazilian Amazon. By comparing species accumulation curves and diversity indices (e.g., using Hill numbers), our approach aims to determine whether comprehensive taxonomic inventories require a combination of methods, and whether functional diversity estimates are robust to methodological biases. This integrated strategy is critical for optimizing biodiversity surveys and for informing effective conservation strategies in one of the world's most biodiverse ecosystems.

2. METHODS

2.1. - Study Area and Design

This study was conducted across 13 locations distributed throughout distinct biogeographic regions of the Brazilian Amazon (Fig. 1). The sampling locations were selected to encompass diverse environmental conditions and fill sampling gaps across major Amazonian interfluviums (Guedes et al., 2018; Carvalho et al., 2023). Surveys were conducted between 2019 and 2023, with fieldwork concentrated during the dry season (May to December) to standardize sampling conditions and maximize detection probability.

Our sampling design followed a hierarchical spatial structure. At the broadest scale, sampling locations were distributed across different biogeographic realms defined by major Amazonian rivers. Within each realm, we established sampling landscapes (designated by two-letter codes, e.g., AA - Amana, TQ - Tumucumaque). Each landscape was divided into three sites (A, B, and C), with each site containing a 1-km linear transect. Sites were positioned with a minimum distance of 1 km between them to ensure spatial independence.

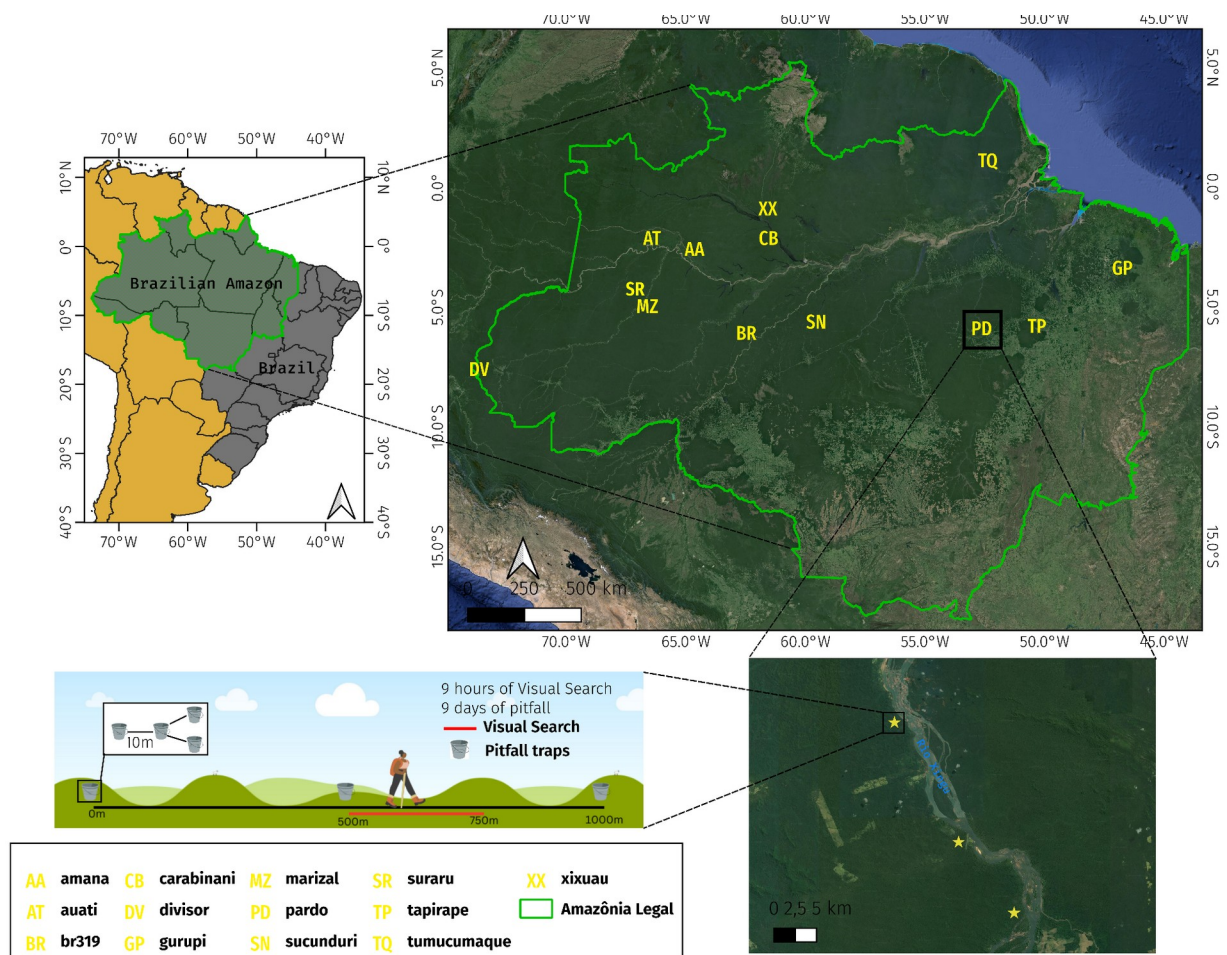


Figure 1 - Sampling points of the ABC expeditions throughout the Brazilian Amazon Forest. Three transects were established in each sampling area. Three pitfall traps were installed along each transect, spaced 500 meters apart. A) Location of the study region within the Amazon basin. B) Location of the sampling areas. C) Location of each transect within the sampling area. D) Schematic drawing of pitfall traps and visual search along the transect.

2.2. - Sampling Methods

We employed three standardized sampling methods to survey squamate reptiles. First, within each site we installed three Y-shaped pitfall trap arrays along the 1-km transect at 0 m, 500 m, and 1,000 m. Each array consisted of four 60-liter buckets—one at the center and one at the end of each of the three 10-meter arms of a drift fence arranged in a Y configuration—with the drift fences serving as barriers that directed moving animals into the buckets. Pitfall traps operated continuously for nine consecutive nights at each site, totaling 1,053 trap-nights across all study sites (Ribeiro-Júnior, Gardner, & Ávila-Pires, 2008).

In addition to pitfall trapping, we conducted systematic active searches. These consisted of visual surveys along a 250-meter section of each site's transect (between the 500-750 m marks) wherein we searched for species within the vegetation and leaf-litter habitats along a 20-meter-wide band (10 meters on each side of the transect line). Two experienced herpetologists performed six surveys per site—three diurnal (16:00–18:00) and three nocturnal (19:00–20:20) sessions—with each survey lasting 40–80 minutes, resulting in approximately 234 person-hours of total search effort (Martins & Oliveira, 1998; Scott, Crump, & Zimmerman, 1994).

Finally, we recorded occasional encounters, which consisted of incidental

observations of squamates made by both the herpetologists and other team members during activities such as transect establishment and movement between sampling points. To maintain spatial consistency with our sampling design, only observations that occurred within the boundaries of our established sites (A, B, or C) were included. All occasional encounters were validated through specimen collection and verified by the project's herpetologists.

To minimize interference between methods, we maintained a minimum distance of 20 meters between pitfall traps and active search areas. Species that could not be identified in the field were collected following standard ethical protocols (Pisani, 1973), fixed in 10% formalin, and preserved in 70% ethanol. Voucher specimens were deposited in the herpetological collections of the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Coleção Herpetológica of the Federal University of Santa Catarina (CHUFSC). Taxonomic identification of all species followed the keys provided by Ávila-Pires (1995), Peters and Donoso-Barros (1970), and Vitt et al. (2007) for lizards, and Ferrarezzi and Monteiro (2001), Peters and Orejas-Miranda (1970), and Zaher (1999) for snakes. Species nomenclature was based on The Reptile Database (Uetz, accessed in 2025).

2.3. - Data Analysis

All analyses were performed in R (version 4.2.2; R Core Team, 2023). We evaluated both diversity patterns and compositional differences among sampling methods for lizards and snakes separately.

We calculated taxonomic and functional diversity using Hill numbers ($q = 0, 1$, and 2) to provide a comprehensive assessment of diversity patterns that accounts for species richness ($q = 0$), common species ($q = 1$), and dominant species ($q = 2$). Taxonomic diversity was calculated using the 'hillR' package (Li, 2018). For functional diversity, we first processed species trait data using the 'FD' package (Laliberté et al., 2014). For lizards, we included traits related to body size, habitat use, and thermoregulation strategy. Snake traits included body mass, diet, activity period, habitat use, and reproductive mode. Trait data were standardized and converted to a distance matrix using the Gower distance metric to account for both continuous and categorical traits.

To assess sampling completeness and compare method efficiency, we constructed species accumulation curves using the 'iNEXT' package (Hsieh et al., 2016). Curves were generated for both individual methods and method combinations, including interpolation (rarefaction) and extrapolation with 95% confidence intervals based on 999 bootstrap replicates.

To test for differences in diversity indices among sampling methods, we used Generalized Linear Mixed Models (GLMMs) implemented through the 'lme4' package (Bates et al., 2015). Models included sampling method as a fixed effect and sampling landscape as a random effect to account for spatial autocorrelation. We used a Gamma distribution with a log link function to account for the non-negative, continuous nature of diversity indices. Post-hoc comparisons were conducted using the 'emmeans' package (Lenth, 2020) with Tukey's adjustment for multiple comparisons.

We examined taxonomic and functional compositional differences among sampling methods using distance-based approaches. For taxonomic composition, we calculated

Jaccard dissimilarity indices using presence-absence data. For functional composition, we used community-weighted mean trait values to calculate Euclidean distances between communities. Both analyses were performed using the 'vegan' package (Oksanen et al., 2013).

We visualized compositional patterns using Principal Coordinates Analysis (PCoA) implemented through the 'ape' package (Paradis & Schliep, 2019). To test for significant differences in composition among methods, we performed Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations using the 'adonis2' function in 'vegan'. Additionally, we tested for homogeneity of multivariate dispersions using the 'betadisper' function to ensure that significant PERMANOVA results were not solely due to differences in dispersion among methods.

To visualize species distribution in functional space, we performed a PCoA on the species trait distance matrix. The resulting ordination illustrates how species are distributed based on their functional traits and helps interpret the functional composition patterns observed across sampling methods.

All visualizations were created using the 'ggplot2' package (Wickham, 2016), with additional customization through 'gridExtra' (Auguie, 2017) for multi-panel figures. Error bars in diversity plots represent standard errors of the mean.

3. RESULTS

3.1. - Sampling Effectiveness

Our sampling effort resulted in 989 lizard and 133 snake records across all sampling methods and locations in the Brazilian Amazon. In total, we recorded 55 lizard species and 56 snake species, with different methods showing varying effectiveness for each group.

For lizards, pitfall traps were the most effective individual method, capturing 45 species (578 individuals), followed by active search with 33 species (319 individuals), and occasional encounters with 30 species (92 individuals). Species accumulation curves revealed distinct patterns of sampling effectiveness between methods (Fig. 2A). Pitfall traps accumulated species more rapidly and reached higher richness estimates than other methods, with their observed richness approaching asymptotic values, suggesting adequate sampling completeness. Active search and occasional encounters showed similar accumulation patterns but with lower total richness. When methods were combined, sampling completeness improved substantially, capturing the total observed diversity of 55 lizard species. The relatively narrow confidence intervals in the combined methods curves indicate reliable richness estimates.

Snake sampling showed markedly different effectiveness patterns. Occasional encounters yielded the highest species richness (43 species from 79 individuals) among individual methods, followed by active search (23 species from 40 individuals), while pitfall traps showed notably lower effectiveness, capturing only 11 species from 14 individuals. Individual method curves for snakes showed steeper trajectories and wider confidence intervals compared to lizards, suggesting incomplete sampling and potential for additional species discovery (Fig. 2B). The combination of methods improved sampling completeness, allowing us to record a total of 56 snake species. However, the extrapolated portions of the accumulation curves and their confidence intervals indicate

that snake inventories might still be incomplete even with combined methods.

The complementarity among methods was evident in both taxa, but more pronounced in snakes. While each individual method showed limitations in capturing the full species diversity, their combination provided a more comprehensive sampling of the squamate community. This complementarity was particularly important for capturing species with different natural histories and habitat use patterns. For instance, while pitfall traps were most effective for lizards, they performed poorly for snakes, while occasional encounters proved most efficient. This pattern highlights the importance of employing multiple methods for comprehensive squamate surveys in tropical forests.

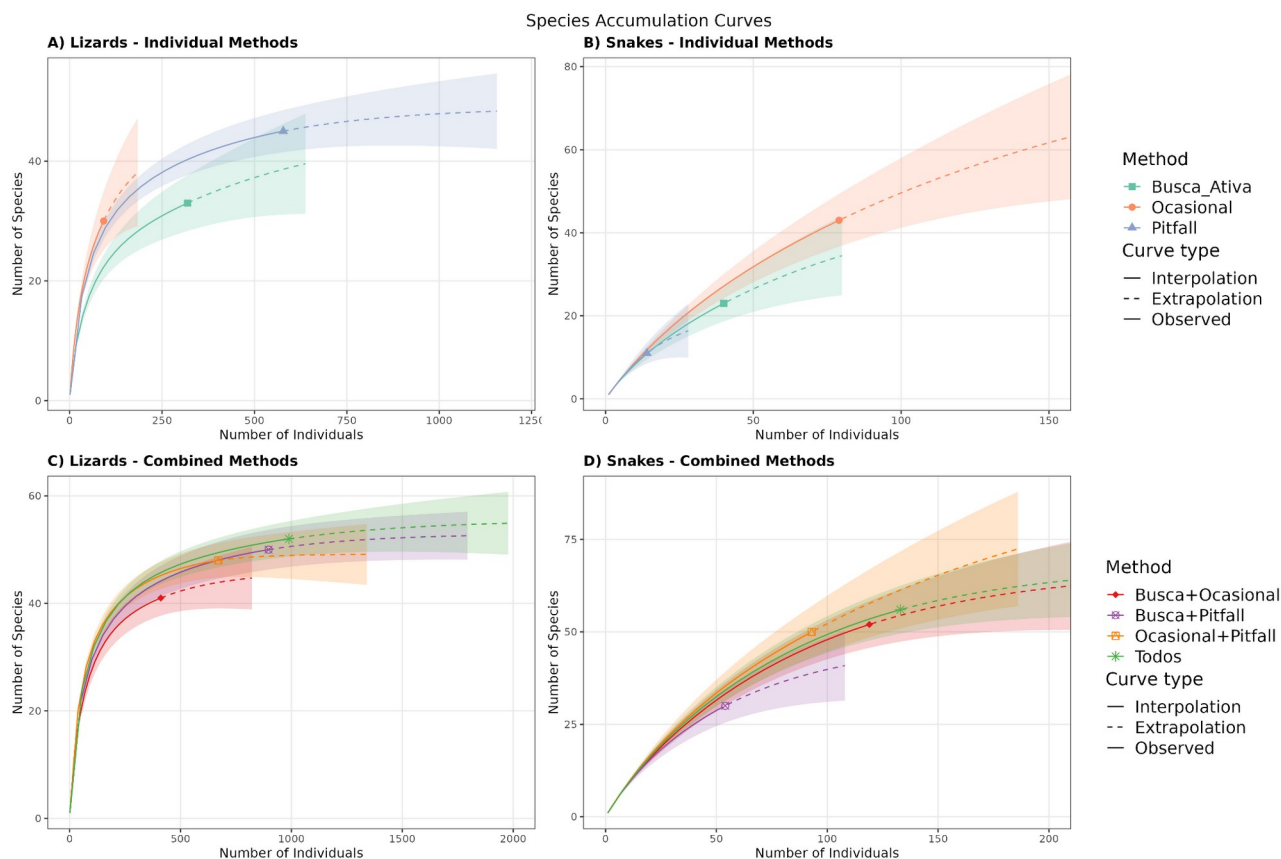


FIG 2 – Species accumulation curves for lizards and snakes in the Brazilian Amazon using different sampling methods. Top panels show curves for individual methods (Pitfall traps, Active search, and Occasional encounters), while bottom panels show curves for method combinations. Solid lines represent interpolation, dashed lines represent extrapolation, and shaded areas represent 95% confidence intervals. Numbers in parentheses indicate the total number of individuals and species recorded for each method or combination.

3.2. - Diversity Patterns

Taxonomic and functional diversity patterns showed distinct responses to sampling methods, with marked differences between lizards and snakes (Fig. 3 & 4, Table S1).

For lizards, taxonomic diversity differed significantly among sampling methods across all Hill numbers ($q = 0$: $p < 0.001$; $q = 1$: $p < 0.001$; $q = 2$: $p < 0.01$). Pitfall traps consistently showed higher taxonomic diversity than other methods. For species richness ($q = 0$), pitfall traps yielded significantly higher values than both active search ($p < 0.01$) and occasional encounters ($p < 0.0001$). This pattern persisted when accounting for common species ($q = 1$) and dominant species ($q = 2$), with pitfall traps maintaining higher diversity values. Active search and occasional encounters showed similar diversity levels,

with no significant differences between them across all q values. In contrast, functional diversity showed no significant differences among sampling methods ($q = 0$: $p = 0.34$; $q = 1$: $p = 0.58$; $q = 2$: $p = 0.67$), suggesting that all methods captured similar ranges of functional traits despite differences in species composition.

Snake diversity patterns revealed an opposite trend. Taxonomic diversity differed significantly among methods ($p < 0.0001$ for all q values), but with occasional encounters showing the highest values. Post-hoc comparisons revealed that occasional encounters yielded significantly higher taxonomic diversity than both active search ($p < 0.01$) and pitfall traps ($p < 0.0001$) across all Hill numbers. Active search consistently showed intermediate diversity values, while pitfall traps captured significantly lower diversity. This pattern was consistent whether considering all species equally ($q = 0$), common species ($q = 1$), or dominant species ($q = 2$). Similar to lizards, functional diversity measures showed no significant differences among sampling methods ($q = 0$: $p = 0.32$; $q = 1$: $p = 0.34$; $q = 2$: $p = 0.35$), indicating that despite varying success in capturing taxonomic diversity, all methods sampled similar ranges of functional traits.

These results reveal that while sampling methods significantly influence our perception of taxonomic diversity, they have limited impact on functional diversity patterns. This suggests that although different methods vary in their ability to capture species richness and abundance, they tend to sample species with similar ranges of functional traits.

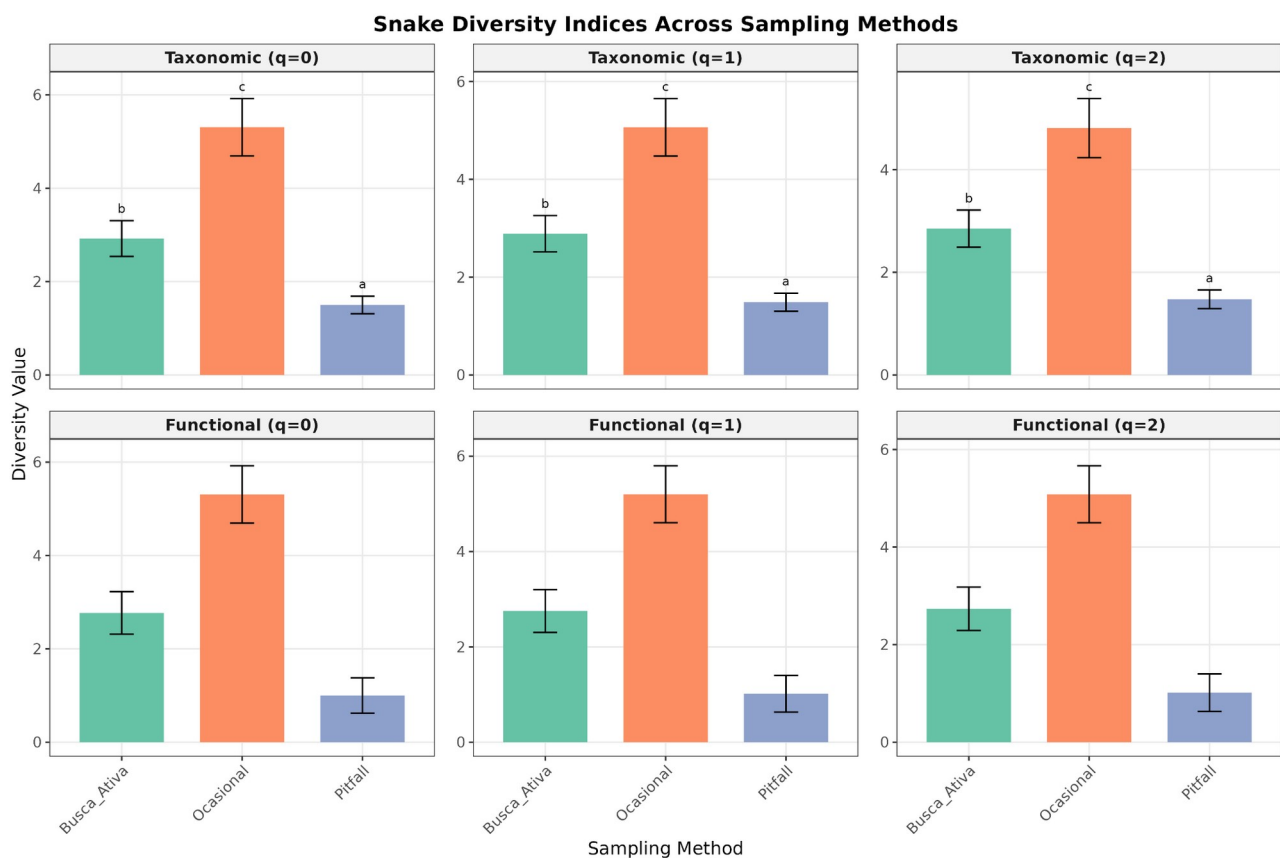


Figure 3 - Taxonomic and functional diversity indices across sampling methods for lizards and in the Brazilian Amazon. Bar plots show Hill numbers at different q values ($q = 0$: species richness; $q = 1$: common species; $q = 2$: dominant species) for both taxonomic and functional diversity. Error bars represent standard errors. Different letters indicate significant differences between sampling methods ($p < 0.05$) based on Gamma GLMM followed by Tukey post-hoc test.

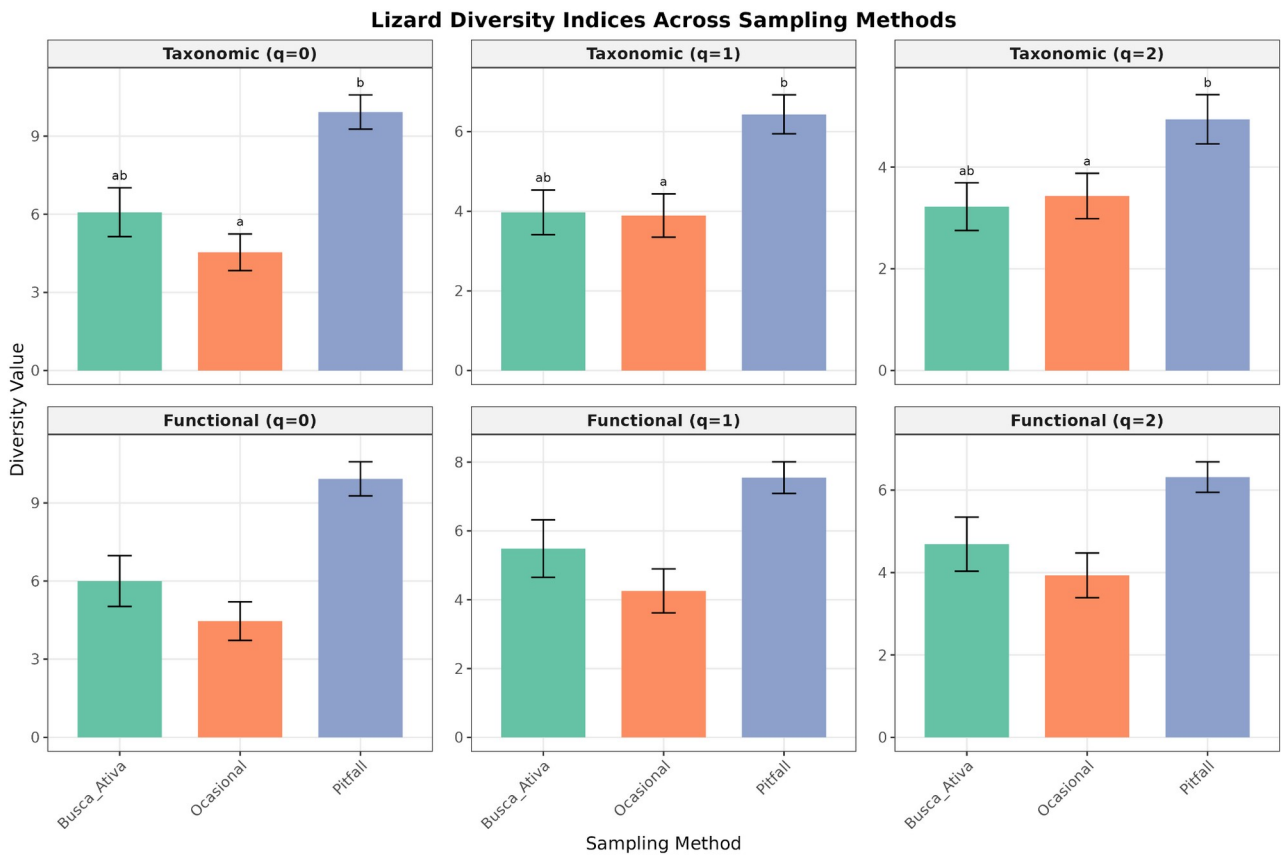


Figure 4 - Taxonomic and functional diversity indices across sampling methods for snakes in the Brazilian Amazon. Bar plots show Hill numbers at different q values ($q = 0$: species richness; $q = 1$: common species; $q = 2$: dominant species) for both taxonomic and functional diversity. Error bars represent standard errors. Different letters indicate significant differences between sampling methods ($p < 0.05$) based on Gamma GLMM followed by Tukey post-hoc test.

3.3. - Compositional Patterns

Taxonomic and functional composition analyses revealed different patterns between sampling methods, with varying effects for lizards and snakes (Fig. 5, Table S2).

For lizards, PERMANOVA indicated significant differences in taxonomic composition among sampling methods ($R^2 = 0.085$, $p = 0.002$). The ordination plot showed moderate overlap between methods, with pitfall traps capturing a distinct subset of species compared to active search and occasional encounters. The dispersion test revealed marginally significant differences in compositional variability among methods ($p = 0.06$), suggesting some heterogeneity in the variation of species composition within each method. In contrast, functional composition showed no significant differences among methods ($R^2 = 0.108$, $p = 0.104$), although there was a marginal difference in functional dispersion ($p = 0.051$). This suggests that while methods sampled different species, they captured similar ranges of functional traits.

Snake assemblages showed similar patterns of compositional differentiation among methods. Taxonomic composition differed significantly among sampling methods ($R^2 = 0.087$, $p = 0.004$), with clear separation between methods in ordination space. Occasional encounters and active search showed some overlap in species composition, while pitfall traps captured a distinct assemblage. Unlike lizards, snake assemblages showed consistent levels of compositional variation within methods, as indicated by non-significant dispersion tests ($p = 0.815$). Functional composition, however, did not differ significantly among methods ($R^2 = 0.070$, $p = 0.337$), and functional dispersion was similar across

methods ($p = 0.121$). This indicates that despite capturing different species, all methods sampled similar portions of the functional trait space.

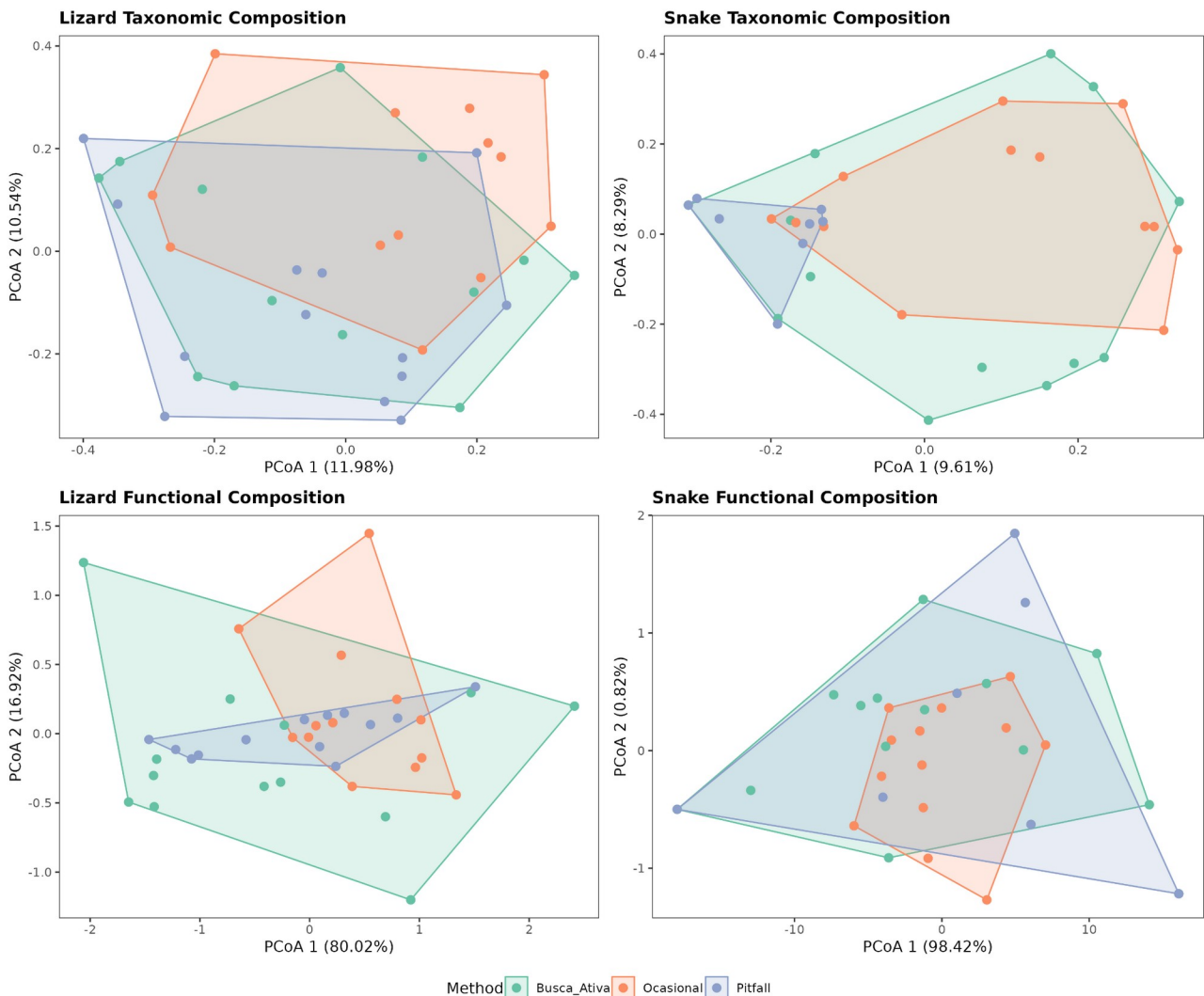


Figure 5 - Composition analysis of lizard and snake assemblages across sampling methods in the Brazilian Amazon. Top panels show taxonomic composition and bottom panels show functional composition based on Principal Coordinates Analysis (PCoA). Colored polygons represent the convex hull of each sampling method. Numbers in parentheses indicate the percentage of variation explained by each axis.

3.4. - Species Distribution in Functional Space

The analysis of species distribution in functional trait space (Fig. 6, supplementary material) revealed distinct patterns for lizards and snakes. For lizards, the ordination showed clear separation between arboreal and terrestrial species (PCoA1 = 85.84%, PCoA2 = 17.87%). The left portion of the functional space was occupied by arboreal species, including *Gonatodes* species (*G. eladioi*, *G. humeralis*, and *G. hasemani*) which utilize both ground and trunk microhabitats as semi-arboreal species, clustered near *Anolis* species that partition different vegetation strata from near-ground to tree trunks. The right portion of the space was dominated by terrestrial species, particularly teiids and scincids.

Snake functional space showed a more continuous distribution of species (PCoA1 = 44.07%, PCoA2 = 35.25%). Large-bodied species such as *Boa constrictor* and *Epicrates cenchria* occupied one extreme of the functional space, while small fossorial species like

Atractus and *Amerotyphlops* occupied the opposite end. Species were arranged along gradients defined by body size, diet, and habitat use, with clear separation between terrestrial (e.g., *Drymarchon corais*) and arboreal species (e.g., *Corallus batesi*). This continuous distribution of functional traits helps explain why different sampling methods, despite their taxonomic biases, captured similar ranges of functional diversity.

This functional organization helps explain why different sampling methods, despite their taxonomic biases, captured similar ranges of functional diversity, as they collectively sampled species across these major ecological strategies.

4. DISCUSSION

Our study reveals that sampling methods significantly influence taxonomic diversity and composition of Amazonian squamates while appearing to have limited impact on functional diversity patterns as measured by our approach. However, this apparent functional stability across methods demands careful interpretation.

The observed pattern of similar functional diversity across sampling methods could reflect two distinct possibilities. First, it may indicate genuine functional redundancy within Amazonian squamate communities, where different species captured by distinct methods fulfill similar ecological roles. This would align with niche-based theories suggesting that hyperdiverse tropical communities may maintain numerous species performing comparable ecological functions (Hubbell, 2001).

Alternatively, this pattern might result from methodological limitations in our functional diversity assessment. The categorical nature of many of our traits may lack sensitivity to detect fine-scale functional differences between species. Our reliance on community-weighted means could potentially mask within-community trait variation, particularly if sampling methods differ in capturing species with extreme trait values but similar averages. Moreover, our choice of functional diversity metrics, primarily based on Hill numbers, may not capture certain dimensions of functional diversity that metrics like Functional Dispersion (FDis) or Rao's Quadratic Entropy might reveal.

To distinguish between these possibilities, future studies should incorporate more refined quantitative trait measurements and employ multiple complementary functional diversity metrics. Additionally, examining functional diversity at finer taxonomic or ecological scales might reveal method-specific biases that are obscured at the community level. The relationship between taxonomic and functional diversity under different sampling regimes represents a critical area for further investigation, with important implications for biodiversity monitoring protocols.

For lizards, pitfall traps proved most effective, capturing not only terrestrial species but also semi-arboreal and arboreal taxa. This unexpected breadth of capture suggests that traditional assumptions about pitfall trap limitations may need revision, at least for Amazonian lizards. The effectiveness of pitfall traps likely results from both the high activity levels of many lizard species (Pianka, 1973; Gotelli & Colwell, 2001) and the continuous sampling nature of the method (Magnusson et al., 2005). Previous studies in tropical forests have similarly found pitfall traps effective for sampling lizard communities (Freitas et al., 2017), although our results show that even these effective methods alone fail to capture complete lizard diversity, emphasizing the need for complementary

approaches. The success of pitfall traps in capturing arboreal species might be related to the frequent descent of these species to the forest floor for foraging or thermoregulation (Vitt et al., 2007), a behavior that merits further investigation.

For snakes, occasional encounters proved most effective, followed by active search, while pitfall traps showed limited success. This pattern is consistent with challenges documented in tropical snake sampling (Doan, 2003; Fraga et al., 2014, Masseli, 2019). Snakes' unpredictable activity patterns and generally low detection probabilities (Gardner et al., 2008) likely account for the superior performance of opportunistic methods in our surveys. The poor performance of pitfall traps for snakes has also been attributed to the ability of many species to escape or avoid traps (Gotelli & Colwell, 2001). These findings underscore the need for long-term and multi-method approaches when studying snake communities.

Interestingly, while sampling methods strongly influenced taxonomic diversity, they had no significant effect on functional diversity patterns. This suggests that each method, despite species-detection biases, captures a representative sample of the community's functional traits. However, this pattern should be interpreted cautiously given that our functional trait data were derived from categorical measures rather than from detailed quantitative analyses (Magurran, 2013). More refined analyses employing quantitative traits might reveal finer-scale differences (Gotelli & Graves, 1996). The disconnect between taxonomic and functional diversity responses implies a degree of functional redundancy within Amazonian squamate communities, where different species perform similar ecological roles (Hubbell, 2001).

For lizards, although pitfall traps detected a higher number of species, the sampled functional trait range was similar to that of results from active search and occasional encounters. Similarly, snake surveys—despite differing in taxonomic outcomes—captured comparable proportions of functional diversity defined along axes of body size, habitat use, and foraging strategy.

These findings have important implications for biodiversity surveys in tropical forests. The effectiveness of pitfall traps for sampling both terrestrial and arboreal lizards challenges conventional notions of method-specific biases. Moreover, while comprehensive taxonomic inventories may require combining multiple methods to overcome detectability issues, functional diversity patterns appear relatively robust regardless of the sampling approach. This suggests that sampling designs could be tailored to research objectives: when documenting overall species richness and community composition, multiple complementary methods are necessary (Peixoto et al., 2019; Pantoja & Fraga et al., 2012); however, broad assessments of ecosystem functionality might be reliably achieved through more streamlined approaches.

Future studies should incorporate quantitative morphological measurements in addition to categorical traits to better resolve functional differences among species. It is also important to examine whether these patterns are consistent across spatial and temporal scales and to explore the underlying mechanisms driving the apparent effectiveness of pitfall traps for arboreal lizards. Such insights will improve sampling protocols for tropical forest surveys and advance our understanding of vertical habitat use patterns in these complex ecosystems.

5. CONCLUSION

Our results indicate that while taxonomic diversity assessments of Amazonian squamates are strongly influenced by the chosen sampling method, functional diversity estimates are comparatively robust. For lizards, pitfall traps capture a broader taxonomic spectrum, whereas snake communities are best documented via opportunistic encounters. The evident taxonomic discrepancies, with method-specific biases, highlight the necessity of a multi-method approach for complete community inventories. At the same time, the similarity in functional trait space among methods suggests that ecosystems may possess an inherent functional redundancy that buffers against under-sampling biases. For practical applications, we recommend that researchers prioritize a combination of sampling techniques for comprehensive taxonomic inventories, while targeted protocols may suffice for functional diversity studies. Future efforts should aim to integrate quantitative trait data and investigate the spatiotemporal robustness of these patterns, thereby further refining methods that underpin conservation strategies in tropical forests.

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7. Supplementary material

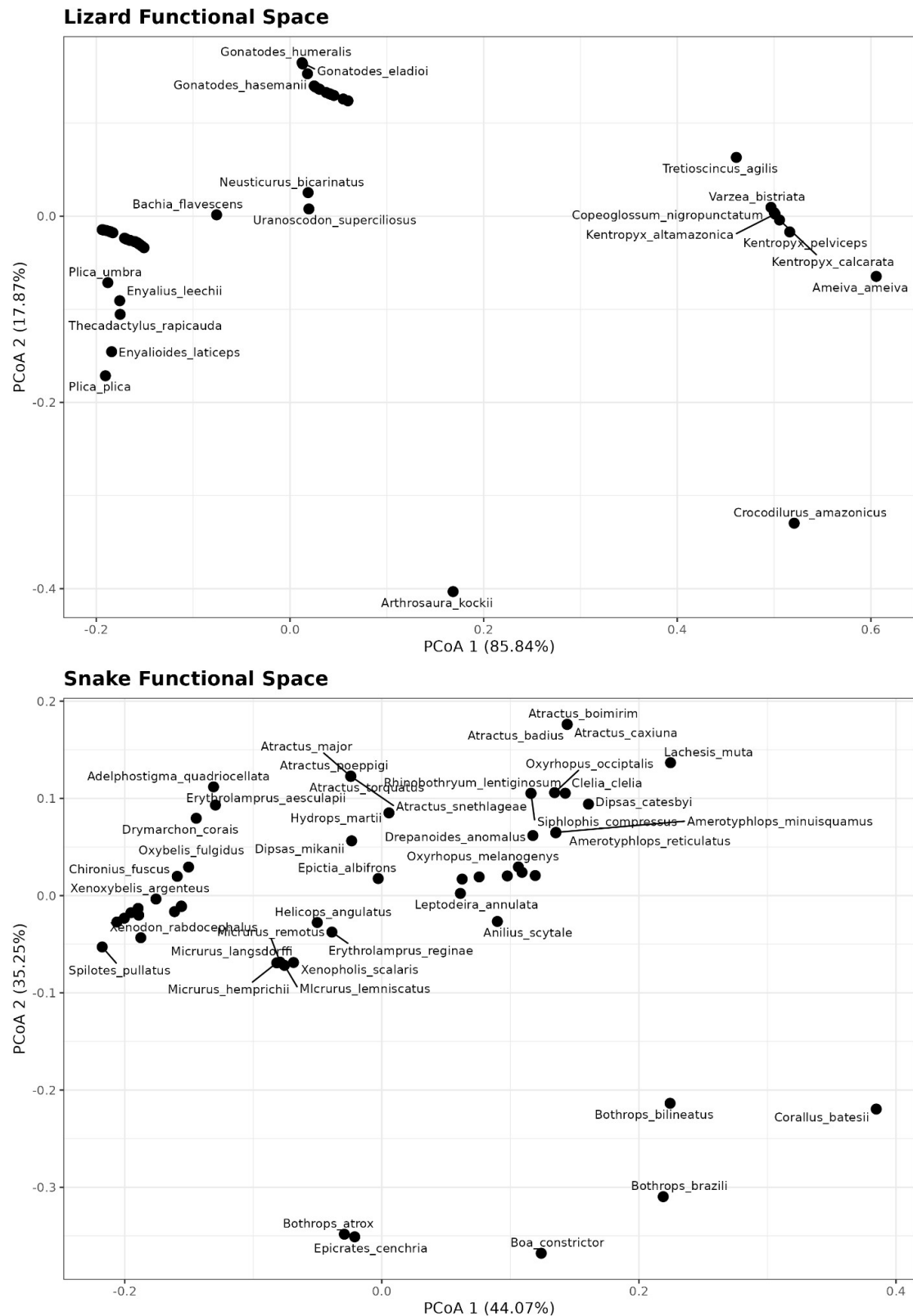


Figure 6. Distribution of species in functional trait space for lizards (left) and snakes (right) in the Brazilian Amazon. Points represent species positions based on Principal Coordinates Analysis (PCoA) of functional traits. Numbers in parentheses indicate the percentage of variation explained by each axis. Species names are shown to illustrate the distribution of different ecological strategies across functional space.

Table S1 - Table S1. Statistical analysis of taxonomic and functional diversity across different sampling methods for lizards and snakes in the Brazilian Amazon. Results show p-values from Generalized Linear Mixed Models (GLMMs) testing the effect of sampling methods on Hill numbers ($q = 0$: species richness; $q = 1$: common species; $q = 2$: dominant species). Post-hoc comparisons show pairwise differences between methods (BA = Active Search, O = Occasional, P = Pitfall). Significant results ($p < 0.05$) are indicated by asterisks (*), while 'ns' indicates non-significant results. NA indicates cases where post-hoc tests were not performed due to non-significant main effects.

Group	Diversity_Type	Hill_Number	P_Value	Post_Hoc
Lizards	Taxonomic	$q=0$	3.05e-04	BA-O: $p=0.2755$; BA-P: $p=0.0063$; O-P: $p<0.0001$
Lizards	Taxonomic	$q=1$	9.57e-04	BA-O: $p=0.0117$; BA-P: $p<0.0001$; O-P: $p<0.0001$
Lizards	Taxonomic	$q=2$	6.27e-03	BA-O: $p=0.8536$; BA-P: $p=0.0045$; O-P: $p=0.0249$
Lizards	Functional	$q=0$	3.39e-01	NA
Lizards	Functional	$q=1$	5.77e-01	NA
Lizards	Functional	$q=2$	6.75e-01	NA
Snakes	Taxonomic	$q=0$	1.36e-06	BA-O: $p=0.0012$; BA-P: $p=0.0017$; O-P: $p<0.0001$
Snakes	Taxonomic	$q=1$	1.86e-06	BA-O: $p=0.0021$; BA-P: $p=0.0014$; O-P: $p<0.0001$
Snakes	Taxonomic	$q=2$	3.14e-06	BA-O: $p=0.0041$; BA-P: $p=0.0015$; O-P: $p<0.0001$
Snakes	Functional	$q=0$	3.23e-01	NA
Snakes	Functional	$q=1$	3.37e-01	NA
Snakes	Functional	$q=2$	3.47e-01	NA

Table S2 - Table S2. Results of PERMANOVA and dispersion tests for taxonomic (Tax.) and functional (Func.) composition among sampling methods. For each analysis, R^2 , F-statistic (F) and p-values are shown. Significance column shows PERMANOVA/Dispersion test results (* $p < 0.05$; ns: non-significant).

Group	Composition	PERMANOVA	Dispersion	Significance
Lizards	Tax.	$R^2 = 0.085$; $F = 1.67$; $p = 2.00e-03$	$F = 3.01$; $p = 7.10e-02$	* / ns
Lizards	Func.	$R^2 = 0.108$; $F = 2.18$; $p = 9.70e-02$	$F = 3.29$; $p = 5.30e-02$	ns / ns
Snakes	Tax.	$R^2 = 0.087$; $F = 1.47$; $p = 5.00e-03$	$F = 0.2$; $p = 8.31e-01$	* / ns
Snakes	Func.	$R^2 = 0.07$; $F = 1.16$; $p = 3.41e-01$	$F = 2.17$; $p = 1.56e-01$	ns / ns

Table S3a - Species list and abundance data for lizards recorded in the Brazilian Amazon. For each species, we present the total abundance and the number of individuals recorded

by each sampling method (Active Search, Occasional Encounters, and Pitfall Traps).

Species	Total Abundance	Active Search	Ocasional	Pitfall
<i>Alopoglossus angulatus</i>	14	4	0	10
<i>Alopoglossus atriventris</i>	26	3	0	23
<i>Alopoglossus brevifrontalis</i>	19	1	1	17
<i>Alopoglossus buckleyi</i>	7	0	2	5
<i>Alopoglossus theodoruse</i>	1	1	0	0
<i>Amapasaurus tetradactylus</i>	9	0	0	9
<i>Ameiva ameiva</i>	13	0	5	8
<i>Anolis chrysolepis</i>	9	5	3	1
<i>Anolis fuscoauratus</i>	29	18	8	3
<i>Anolis ortonii</i>	1	1	0	0
<i>Anolis planiceps</i>	1	0	0	1
<i>Anolis punctatus</i>	6	2	3	1
<i>Anolis sypheus</i>	14	3	6	5
<i>Anolis tandai</i>	47	12	16	19
<i>Anolis trachyderma</i>	4	2	2	0
<i>Anolis transversalis</i>	9	3	4	2
<i>Arthrosaura kockii</i>	29	7	1	21
<i>Arthrosaura reticulata</i>	40	1	3	36
<i>Bachia flavescens</i>	5	0	0	5
<i>Cercosaura anordosquama</i>	4	0	1	3
<i>Cercosaura argulus</i>	12	0	2	10
<i>Cercosaura bassleri</i>	7	1	2	4
<i>Cercosaura ocellata</i>	7	0	0	7
<i>Cercosaura olivacea</i>	2	0	0	2
<i>Cercosaura oshaughnessyi</i>	2	0	0	2
<i>Chatogekko amazonicus</i>	129	108	2	19
<i>Coleodactylus meridionalis</i>	7	7	0	0

<i>Copeoglossum nigropunctatum</i>	24	7	3	14
<i>Crocodilurus amazonicus</i>	2	0	1	1
<i>Enyaliodes laticeps</i>	9	6	1	2
<i>Enyalius leechii</i>	3	1	1	1
<i>Gonatodes annularis</i>	3	0	0	3
<i>Gonatodes eladioi</i>	1	1	0	0
<i>Gonatodes hasemanii</i>	2	0	0	2
<i>Gonatodes humeralis</i>	43	23	5	15
<i>Iphisa elegans</i>	29	7	1	21
<i>Iphisa soinii</i>	2	0	0	2
<i>Kentropyx altamazonica</i>	6	0	0	6
<i>Kentropyx calcarata</i>	43	3	1	39
<i>Kentropyx pelviceps</i>	130	10	6	114
<i>Loxopholis guianense</i>	81	40	0	41
<i>Loxopholis osvaldoi</i>	14	8	0	6
<i>Loxopholis percarinatum</i>	19	1	1	17
<i>Loxopholis snethlageae</i>	42	7	0	35
<i>Neusticurus bicarinatus</i>	1	0	1	0
<i>Plica plica</i>	11	0	3	8
<i>Plica umbra</i>	33	18	1	14
<i>Pseudogonatodes guianensis</i>	19	2	1	16
<i>Thecadactylus rapicauda</i>	6	5	0	1
<i>Tretioscincus agilis</i>	7	1	0	6
<i>Uranoscodon superciliosus</i>	5	0	5	0
<i>Varzea bistrata</i>	1	0	0	1

Table S4b - Species list and abundance data for snakes recorded in the Brazilian Amazon. For each species, we present the total abundance and the number of individuals recorded by each sampling method (Active Search, Occasional Encounters, and Pitfall Traps).

Species	Total_Abundance	Busca_Ativa	Ocasional	Pitfall
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<i>Adelphostigma quadriocellata</i>	1	0	1	0
<i>Amerotyphlops minuisquamus</i>	1	0	1	0
<i>Amerotyphlops reticulatus</i>	2	0	0	2
<i>Anilius scytale</i>	1	0	1	0
<i>Apostolepis nigrolineata</i>	1	0	1	0
<i>Atractus badius</i>	1	0	1	0
<i>Atractus boimirim</i>	2	1	0	1
<i>Atractus caxiuna</i>	1	0	1	0
<i>Atractus major</i>	2	1	1	0
<i>Atractus poeppigi</i>	1	0	0	1
<i>Atractus snethlageae</i>	2	0	1	1
<i>Atractus torquatus</i>	3	0	2	1
<i>Boa constrictor</i>	3	0	3	0
<i>Bothrops atrox</i>	14	3	11	0
<i>Bothrops bilineatus</i>	2	1	1	0
<i>Bothrops brazili</i>	1	0	1	0
<i>Chironius exoletus</i>	2	2	0	0
<i>Chironius fuscus</i>	2	0	2	0
<i>Chironius multiventris</i>	2	0	2	0
<i>Chlorosoma viridissimum</i>	1	0	1	0
<i>Clelia clelia</i>	4	1	2	1
<i>Corallus batesii</i>	2	1	1	0
<i>Dendrophidion dendrophis</i>	2	0	2	0
<i>Dipsas catesbyi</i>	3	2	1	0
<i>Dipsas mikanii</i>	1	0	1	0
<i>Drepanoides anomalus</i>	4	3	0	1
<i>Drymarchon corais</i>	1	0	1	0
<i>Epicrates cenchria</i>	5	1	4	0
<i>Epictia albifrons</i>	2	0	2	0

<i>Erythrolamprus aesculapii</i>	1	0	1	0
<i>Erythrolamprus oligolepis</i>	3	0	1	2
<i>Erythrolamprus reginae</i>	2	0	2	0
<i>Erythrolamprus typhlus</i>	4	1	3	0
<i>Helicops angulatus</i>	1	0	0	1
<i>Hydrops martii</i>	1	0	1	0
<i>Imantodes cenchoa</i>	12	7	5	0
<i>Lachesis muta</i>	1	0	1	0
<i>Leptodeira annulata</i>	2	2	0	0
<i>Micrurus lemniscatus</i>	1	1	0	0
<i>Micrurus hemprichii</i>	3	1	0	2
<i>Micrurus langsdorffi</i>	1	0	1	0
<i>Micrurus paraensis</i>	1	0	0	1
<i>Micrurus remotus</i>	2	1	1	0
<i>Oxybelis aenus</i>	1	1	0	0
<i>Oxybelis fulgidus</i>	2	0	2	0
<i>Oxyrhopus melanogenys</i>	2	1	1	0
<i>Oxyrhopus occipitalis</i>	4	0	4	0
<i>Oxyrhopus petolarius</i>	2	1	1	0
<i>Rhinobothryum lentiginosum</i>	1	0	1	0
<i>Siphlophis cervinus</i>	2	1	1	0
<i>Siphlophis compressus</i>	4	4	0	0
<i>Spilotes pullatus</i>	4	1	3	0
<i>Taeniophalus brevirostris</i>	1	0	1	0
<i>Xenodon rabdocephalus</i>	3	0	3	0
<i>Xenopholis scalaris</i>	2	2	0	0
<i>Xenoxybelis argenteus</i>	1	0	1	0

6. CONCLUSÃO

Nesta tese, buscamos ampliar o entendimento dos mecanismos que estruturam as assembléias de Squamata – lagartos e serpentes – em regiões da Amazônia Brasileira, adotando uma abordagem integrada que abrange a influência de gradientes ambientais, dinâmicas temporais e os efeitos dos métodos de amostragem sobre a diversidade taxonômica e funcional. Nossos estudos evidenciam a complexidade dos processos ecológicos e metodológicos que moldam essas comunidades, entregando subsídios para estratégias de conservação em um dos ecossistemas mais diversos e ameaçados do planeta.

No primeiro capítulo, analisamos os padrões temporais de comunidades de Squamata na Floresta Nacional de Carajás, a partir de levantamentos realizados entre 2015 e 2022. Nossos resultados indicaram que as assembléias de lagartos respondem fortemente a variáveis ambientais como a densidade da vegetação e a elevação, apresentando maior abundância e riqueza em áreas de vegetação densa e topografia variada. Em contraste, as serpentes demonstraram respostas mais sutis, com a elevação emergindo como o principal preditor de sua distribuição. Observou-se também uma tendência preocupante de redução na abundância de lagartos após 2019, sugerindo a ocorrência de impactos ou mudanças nos padrões de atividade que merecem uma atenção adicional para futuras pesquisas.

No segundo capítulo, exploramos a influência de variáveis climáticas (temperatura, precipitação e sua sazonalidade), da estrutura da vegetação (altura do dossel e densidade de árvores), dos nutrientes do solo e da proximidade à água (representada pelo HAND) em 13 locais de florestas terra firme. Este estudo permitiu identificar que, para os lagartos, fatores como a proximidade à água, a fertilidade do solo, um dossel elevado e temperaturas máximas mais altas contribuem para maiores abundâncias e enriquecem a riqueza de espécies, com a sazonalidade da temperatura desempenhando um papel crucial na formação das assembléias. Para as serpentes, altos níveis de precipitação durante o período úmido estão associados a menores abundâncias, revelando desafios na amostragem e na compreensão das dinâmicas desse grupo.

No terceiro capítulo, comparamos três métodos de amostragem – pitfall traps com drift fences, active search e encontros ocasionais – para estimar a diversidade taxonômica e funcional de lagartos e serpentes. Os resultados demonstraram que, enquanto as armadilhas pitfall se mostraram mais eficazes para capturar uma ampla gama de lagartos, resultando em maior riqueza e número de indivíduos, os encontros ocasionais foram os mais produtivos para as serpentes. Apesar dessas diferenças significativas na detecção e composição taxonômica entre os métodos, as medidas de diversidade funcional apresentaram valores semelhantes, sugerindo que, mesmo diante de vieses na coleta, a gama de traços ecológicos amostrada permanece consistente em toda a comunidade.

Em síntese, os três estudos integrados desta tese demonstram que gradientes ambientais e variações temporais exercem papel crucial na formação e

manutenção das assembléias de Squamata na Amazônia. Embora a escolha do método de amostragem afete fortemente os inventários taxonômicos, as avaliações de diversidade funcional se mostram robustas e indicam uma redundância funcional significativa. Estes achados sublinham a importância de abordagens integradas e multi-metodológicas para a obtenção de inventários completos e para o desenvolvimento de estratégias de conservação que considerem tanto a complexidade ambiental quanto as limitações metodológicas inerentes aos estudos em ecossistemas tropicais.

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