UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

ESTRUTURA DA PAISAGEM COMO PREDITOR DA DIVERSIDADE TAXONÔMICA E FUNCIONAL DE ANFÍBIOS NA MATA ATLÂNTICA

MAURÍCIO HUMBERTO VANCINE

Rio Claro – SP
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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia, Evolução e Biodiversidade.

Orientador: Dr. Milton Cezar Ribeiro

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TÍTULO DA TESE: ESTRUTURA DA PAISAGEM COMO PREDITOR DA DIVERSIDADE TAXONÔMICA E FUNCIONAL DE ANFÍBIOS NA MATA ATLÂNTICA

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Fonte: BECK, 2018, p. 39.

RESUMO

A perda e fragmentação de habitat devido a mudanças no uso e cobertura da terra por ações antrópicas são uma das principais causas da perda de biodiversidade em todo o mundo. Essas modificações envolvem perda, fragmentação e degradação do habitat. A atuação conjunta desses processos altera as características da paisagem, impactando múltiplos componentes da biodiversidade, como a diversidade taxonômica, genética, filogenética e funcional nas comunidades. Os anfíbios estão entre os organismos mais influenciados pelas características do ambiente, principalmente devido aos seus atributos morfológicos, fisiológicos e ecológicos intrínsecas. A Mata Atlântica contém mais de 720 espécies de anfíbios, das quais mais de 500 espécies (cerca de 70%) são endêmicas, sendo que 46 espécies se encontram em algum grau de ameaça de extinção, principalmente devido à agricultura e expansão urbana. Porém, apesar das intensas mudanças na cobertura e uso da terra na Mata Atlântica nos últimos 50 anos, poucos estudos analisaram a estrutura da paisagem num contexto espaço-temporal para grandes escalas de tempo para esse bioma. Tendo em vista essas questões, nesta tese, respondemos a duas questões principais, estruturada em quatro capítulos: (1) uma envolvendo a dinâmica espaço-temporal da estrutura da paisagem de todo o bioma da Mata Atlântica, e outra (2) em como estrutura da paisagem afeta as dimensões taxonômicas e funcionais de comunidades de anuros neste mesmo bioma. Relacionado a cada uma dessas questões, nós organizamos parte dos dados reunidos e tornamos os mesmos disponíveis para a toda a comunidade científica, por meio de dois data papers: (3) o primeiro com 500 rasters das informações de métricas de paisagem, topografia, hidrografia e antrópicas (ATLANTIC SPATIAL); e (4) o segundo com atributos funcionais morfológicos e ecológicos de parte da diversidade de anfíbios ao longo de toda a Mata Atlântica (ATLANTIC AMPHIBIAN TRAITS). O primeiro capítulo destacou a importância da legislação e da análise da dinâmica da paisagem para auxiliar nos futuros programas de conservação e restauração da biodiversidade na Mata Atlântica. O segundo capítulo gerou dados que permitem a integração eficiente de dados ambientais e de biodiversidade, assim como planejamento da paisagem, conservação da biodiversidade e programas de restauração florestal na Mata Atlântica. O terceiro capítulo demonstrou que a quantidade de habitat florestal, assim como a quantidade de habitat aquático e a conexão entre ambos são fundamentais para a manter múltiplos aspectos da diversidade de anuros na Mata Atlântica. E por fim, o quarto capítulo disponibiliza um valioso conjunto de dados para o avanço de pesquisas sobre os impactos antrópicos e das alterações climáticas na diversidade funcional dos anfíbios na Mata Atlântica.

Palavras-chave: Fragmentação de habitat. Desconexão de habitat. Mata Atlântica. Anfíbios. Diversidade Funcional.

ABSTRACT

Habitat loss and fragmentation due to changes in land use and cover due to human actions are one of the main causes of biodiversity loss worldwide. These modifications involve habitat loss, fragmentation, and degradation. The joint action of these processes changes the characteristics of the landscape, impacting multiple components of biodiversity, such as taxonomic, genetic, phylogenetic, and functional diversity in communities. Amphibians are among the organisms most influenced by the characteristics of the environment, mainly due to their intrinsic morphological, physiological, and ecological attributes. The Atlantic Forest contains more than 720 species of amphibians, of which more than 500 species (around 70%) are endemic, with 46 species facing some degree of threat of extinction, mainly due to agriculture and urban expansion. However, despite the intense changes in land cover and use in the Atlantic Forest in the last 50 years, few studies have analyzed the landscape structure in a spatio-temporal context for large time scales for this biome. Bearing these questions in mind, in this thesis, we answer two main questions, structured in four chapters: (1) one involving the spatio-temporal dynamics of the landscape structure of the entire Atlantic Forest biome, and another (2) on how the structure of the landscape affects the taxonomic and functional dimensions of anuran communities in this same biome. Related to each of these questions, we organized part of the data gathered and made it available to the entire scientific community, through two data papers: (3) the first with 500 rasters of information on landscape metrics, topography, hydrography and anthropic (ATLANTIC SPATIAL); and (4) the second with morphological and ecological functional attributes of part of the diversity of amphibians throughout the entire Atlantic Forest (ATLANTIC AMPHIBIAN TRAITS). The first chapter highlighted the importance of legislation and analysis of landscape dynamics to assist in future biodiversity conservation and restoration programs in the Atlantic Forest. The second chapter generated data that allows the efficient integration of environmental and biodiversity data, as well as landscape planning, biodiversity conservation and forest restoration programs in the Atlantic Forest. The third chapter demonstrated that the amount of forest habitat, as well as the amount of aquatic habitat and the connection between them are fundamental to maintaining multiple aspects of anuran diversity in the Atlantic Forest. And finally, the fourth chapter provides a valuable set of data to advance research on the impacts of anthropic and climate change on the functional diversity of amphibians in the Atlantic Forest.

Keywords: Habitat fragmentation. Habitat split. Atlantic Forest. Amphibians. Functional Diversity.

SUMÁRIO

INTRODUÇÃO GERAL

A perda e fragmentação de habitat devido a mudanças no uso e cobertura da terra por ações humanas são uma das principais causas da perda de biodiversidade em todo o mundo (CHASE et al., 2020; DAVISON; RAHBEK; MORUETA-HOLME, 2021). Essas modificações envolvem a redução da quantidade total de habitat (perda de habitat), subdivisão do habitat em manchas (fragmentação do habitat), alterações na qualidade do habitat (degradação do habitat) e a introdução de outra classe de cobertura da terra (geralmente antrópica) que substitui a habitat perdido (BANKS-LEITE et al., 2020; HADDAD et al., 2015). A atuação conjunta desses processos gera efeitos diretos e indiretos sobre a estrutura da paisagem, alterando sua composição e configuração, reduzindo a área de habitat e aumentando o isolamento e os efeitos de borda sobre a biodiversidade (FAHRIG, 2003, 2017). Em conjunto, esses efeitos alteraram as características da paisagem, como a quantidade/qualidade do habitat e a permeabilidade para as espécies, o que pode impactar múltiplos componentes da biodiversidade, como a diversidade taxonômica, genética, filogenética e funcional nas comunidades (FAHRIG, 2017; FAHRIG et al., 2019; FLETCHER et al., 2018; MILLER-RUSHING et al., 2019).

Há diferentes formas de se mensurar e analisar a diversidade nas comunidades, como as dimensões taxonômica, funcional e filogenética (CIANCIARUSO; SILVA; BATALHA, 2009; CISNEROS et al., 2014; STEVENS; TELLO, 2014). A dimensão taxonômica é mensurada por índices que consideram o número e/ou composição de espécies através da identificação taxonômica das mesmas, avaliando sua incidência ou abundância (MAGURRAN; MCGILL, 2011). A dimensão funcional reflete a variabilidade dos atributos ecológicos das espécies (e.g. morfologia, fisiologia ou história de vida) em relação ao funcionamento dos ecossistemas (PETCHEY; GASTON, 2006). Já a dimensão filogenética representa as diferenças evolutivas entre as espécies desde a divergência de um ancestral comum (FAITH, 1992), refletindo as diferenças ecológicas e fenotípicas filogeneticamente conservadas entre as espécies (CAVENDER-BARES et al., 2009). A análise simultânea dessas dimensões da biodiversidade ao longo dos gradientes ambientais fornece informações fundamentais sobre os mecanismos ecológicos e evolutivos que estruturam os diferentes componentes da diversidade, aumentando o espectro de entendimento do mesmo nas comunidades (CISNEROS et al., 2014; MOUILLOT et al., 2013).

Embora a maioria dos estudos tenha demonstrado os efeitos das modificações na paisagem sobre a diversidade taxonômica (BANKS-LEITE et al. 2014; PALMEIRIM et al.

2019; PÜTTKER et al. 2020; RIOS et al. 2021b), referindo-se ao número ou à composição de espécies em uma comunidade ecológica, uma ampla gama de estudos também demonstrou esses efeitos na redução da diversidade funcional (FLYNN et al. 2009; NOWAKOWSKI et al. 2017; LIU et al. 2018; HATFIELD et al. 2018; SUÁREZ-CASTRO et al. 2020). Por exemplo, a quantidade de habitat, o tamanho dos fragmentos e a heterogeneidade da paisagem foram os principais preditores da diversidade funcional de aves com base na morfologia (por exemplo, massa corporal, índice de asa-mão e largura do bico), dieta, comportamento de forrageamento, reprodução, migração e período de atividade (DE COSTER et al. 2015; BOVO et al. 2018; MATUOKA et al. 2020; BONFIM et al. 2021; FUZESSY et al. 2024; MORENO et al. 2024). O tamanho dos fragmentos e a quantidade de habitat explicaram a diversidade funcional de mamíferos pequenos, médios e grandes em termos de morfologia (por exemplo, massa corporal, comprimento da cauda e forma de locomoção), comportamento, dieta e sensibilidade ambiental (MAGIOLI et al. 2015, 2021; BOVENDORP et al. 2019; RIOS et al. 2021a). Além disso, a quantidade de habitat e os efeitos de borda explicaram a redução da diversidade funcional de anuros ligada aos traços de habitat e reprodução (ALMEIDA-GOMES; ROCHA 2015; FERREIRA et al. 2016; ALMEIDA-GOMES et al. 2019).

Os anfíbios estão entre os organismos mais influenciados pelas características do ambiente, principalmente devido aos seus atributos morfológicos, fisiológicos e ecológicos particulares (MORENO-RUEDA; COMAS, 2023; POUGH et al., 2015). Por exemplo, os anfíbios geralmente têm tamanho corporal pequeno e capacidade limitada de dispersão e locomoção, e são dependentes da respiração cutânea, que geralmente requer alta permeabilidade da pele, tornando-os sensíveis a pequenas mudanças nas condições microclimáticas (MORENO-RUEDA; COMAS, 2023; WELLS, 2007). A maioria das espécies de anfíbios possui ciclo de vida bifásico (larval-aquático e adulto-terrestre), com alta dependência de umidade e/ou disponibilidade de água para sua reprodução (DUELLMAN; TRUEB, 1994). Além disso, por habitarem a interface de ambientes aquáticos e terrestres, os anfíbios tiverem diversas formas de reprodução selecionados ao longo da sua evolução, explicando a alta divergência e diversidade dos modos reprodutivos (CRUMP, 2015; HADDAD; PRADO, 2005; NUNES-DE-ALMEIDA; HADDAD; TOLEDO, 2021). Essas especificidades de habitat envolvem quase sempre a transição entre diferentes tipos de habitat e uma elevada dependência de micro-habitat específicos para reprodução (BECKER et al., 2007, 2010a). Em decorrência dessas particularidades, as modificações da paisagem, principalmente a perda de habitat, são apontadas como uma das principais causas para o

declínio mundial das populações de anfíbios (CUSHMAN, 2006; GRANT; MILLER; MUTHS, 2020; GREEN et al., 2020; LUEDTKE et al., 2023).

A Mata Atlântica contém mais de 720 espécies de anfíbios, das quais mais de 500 espécies (cerca de 70%) são endêmicas (FIGUEIREDO et al., 2021), sendo que 46 espécies se encontram em algum grau de ameaça de extinção, principalmente devido à agricultura e expansão urbana (ANUNCIAÇÃO et al., 2024). Porém, atualmente a Mata Atlântica apresenta 23% de sua extensão original de floresta, com 97% de fragmentos <50 ha, altamente isolados (~800 m) e com alto efeito de estradas e ferrovias (VANCINE et al., 2024). Isso tem resultados em uma grande perda de biodiversidade e de biomassa (DE LIMA et al., 2020, 2024), e apesar da estabilidade e do aumento da cobertura florestal, as florestas antigas estão sendo substituídas por florestas jovens, o que pode estar causando uma grande perda na qualidade do habitat (DIAS; SILVEIRA; FRANCISCO, 2023; PIFFER et al., 2022; ROSA et al., 2021; VANCINE et al., 2024). Embora a diversidade e o endemismo dos anfíbios sejam elevados, o elevado grau de perda, fragmentação e conversão de habitat e micro-habitat sugere que uma parcela significativa dessa diversidade está em vias de ser extirpada da Mata Atlântica (ALMEIDA-GOMES; ROCHA, 2014; HADDAD; PRADO, 2005). Este alto nível de perda e fragmentação de habitat pode ser o mecanismo direto ou indireto por trás do declínio populacional das espécies (ANUNCIAÇÃO et al., 2024; BECKER et al., 2010a; TOLEDO et al., 2023), o que pode comprometer o funcionamento dos ecossistemas aquáticos e terrestres (NOWAKOWSKI et al., 2017; WHILES et al., 2006) ao longo da Mata Atlântica, uma vez que os anfíbios tendem a ser ótimos bioindicadores (VENTURINO et al., 2003).

Os anfíbios possuem vários modos reprodutivos descritos mundialmente (NUNES-DE-ALMEIDA; HADDAD; TOLEDO, 2021), a maioria deles pode ser encontrada na Mata Atlântica, tornando este um aspecto fundamental da história de vida e da diversidade dessas espécies neste bioma (HADDAD; PRADO, 2005). Essa grande diversidade de guildas reprodutivas tem respostas diferentes às modificações da paisagem (ALMEIDA-GOMES; ROCHA, 2015; FERREIRA; BEARD; CRUMP, 2016). Espécies com reprodução aquática, que possuem fase larval aquática (girinos) e fase adulta terrestre dependente de florestas precisam migrar entre esses habitats em diversos momentos de sua vida, e assim são mais afetadas pela desconexão de habitat (Habitat Split) e pela distância de conexão (Split Distance) (BECKER et al., 2007, 2010a, 2010b; FONSECA et al., 2013; LION; GARDA; FONSECA, 2014). Guildas reprodutivas que não possuem estágio larval ou que os adultos não migram entre diferentes habitats, tendem a ser mais afetadas pelo tamanho da mancha e/ou efeitos de borda, como espécies que se reproduzem em bromélias ou diretamente na

serapilheira (DIXO; MARTINS, 2008; DIXO; METZGER, 2010; FERREIRA; BEARD; CRUMP, 2016). Além disso, a desconexão de habitat possui efeitos sobre a incidência de doenças infecciosas, como o fungo *Batrachochytrium dendrobatidis* (BECKER et al., 2023). Dessa forma, para entender como as comunidades podem estar sendo estruturadas em paisagens fragmentadas, é fundamental considerar as diferentes respostas das guildas reprodutivas às diferentes métricas da paisagem (ALMEIDA-GOMES et al., 2022; ALMEIDA-GOMES; ROCHA, 2014, 2015; TODD et al., 2009; WERNER et al., 2007).

Atualmente, as principais ameaças à diversidade de anfíbios são as conversões da cobertura e uso da terra, mudanças climáticas e doenças infecciosas (HOF et al., 2011), com perdas de diversidade funcional e filogenética em comunidades de anfíbios em todo o mundo (NOWAKOWSKI et al., 2017, 2018). Na Mata Atlântica, diversos estudos têm demonstrado os efeitos negativos das modificações das paisagens sobre a diversidade de comunidades de anfíbios em escala local. Por exemplo, diversos temas têm sido abordados nesse sentido, como a composição das comunidades (ALMEIDA-GOMES; ROCHA, 2014; ALMEIDA-GOMES; ROCHA; VIEIRA, 2016; FERREIRA; BEARD; CRUMP, 2016), diversidade funcional (ALMEIDA-GOMES et al., 2019; ALMEIDA-GOMES; ROCHA, 2015), diversidade genética (DIXO et al., 2009) e desconexão de habitat (BECKER et al., 2007, 2010b; LION; GARDA; FONSECA, 2014). Apesar desses trabalhos, ainda há uma lacuna de conhecimento em entender como a estrutura da paisagem funciona como preditor da estruturação das comunidades de anfíbios em todo o bioma, analisando as diferentes dimensões da diversidade, como, por exemplo, taxonômica, funcional e filogenética. Esses resultados podem ser usados para proposição e espacialização de medidas de conservação das espécies de anfíbios no bioma.

Apesar das intensas mudanças na cobertura e uso da terra na Mata Atlântica nos últimos 50 anos (DEAN, 1996; LIRA; PORTELA; TAMBOSI, 2021; SOLÓRZANO; BRASIL; DE OLIVEIRA, 2021), poucos estudos analisaram a estrutura da paisagem num contexto espaço-temporal para grandes escalas de tempo para esse bioma. No estudo mais abrangente até então, Ribeiro et al. (2009) mostraram que restava apenas entre 11 e 16% da cobertura florestal em 2005, da qual 83% estava concentrada em fragmentos menores que 50 hectares, e metade de todas as florestas estavam a menos de 100 m de suas bordas. Adicionalmente, Tabarelli et al. (2010) e Ribeiro et al. (2011) mostraram que uma grande proporção de florestas permanecia em altitudes elevadas (>1600 m). Com base em dados de satélite em escala mais precisa (resolução espacial de 5 m), Rezende et al. (2018) estimou 28% da cobertura vegetal na Mata Atlântica. Em estudos mais recentes, utilizando dados do

MapBiomas (SOUZA et al., 2020), Bicudo da Silva et al. (2020) mostraram que a composição da paisagem não mudou substancialmente entre 1985 e 2018, e que a perda em áreas de vegetação montanhosa foi menor do que em altitudes mais baixas. Além disso, Rosa et al. (2021) mostraram que a relativa estabilidade temporal da cobertura florestal nativa da Mata Atlântica (28 Mha) nos últimos anos foi de devida à substituição de florestas nativas antigas em terrenos mais planos por florestas mais jovens em áreas agrícolas marginais, resultando em maior isolamento entre fragmentos florestais.

Mesmo com esses estudos, existia ainda uma grande necessidade de uma compreensão refinada de como a estrutura da paisagem variou ao longo do tempo na Mata Atlântica. Atualmente, iniciativas brasileiras como o MapBiomas vêm mapeando o uso e a mudança de cobertura da terra com ampla cobertura temática, alta resolução espaço-temporal e classificação padronizada (SOUZA et al., 2020). Isso tem permitido o cálculo e comparação de métricas de paisagem para grandes extensões territoriais e períodos para compreender a dinâmica da paisagem de grandes regiões e biomas inteiros, como a Mata Atlântica e Cerrado (BICUDO DA SILVA et al., 2020; POMPEU; ASSIS; OMETTO, 2023; ROSA et al., 2021; VANCINE et al., 2023, 2024). Além disso, a Mata Atlântica tem uma elevada densidade de infraestruturas lineares (e.g., rodovias, ferrovias, linhas de transmissão de energia e oleodutos e gasodutos) devido à sua elevada (e crescente) população humana e ao desenvolvimento industrial. Essas infraestruturas lineares têm um impacto severo na conectividade da vegetação natural e sobre a biodiversidade (por exemplo, através do desmatamento, perturbações sonoras, poluição e atropelamentos) (CASSIMIRO; RIBEIRO; ASSIS, 2023; MARTINEZ PARDO et al., 2023), mas esses efeitos nunca foram analisados no contexto da estrutura da paisagem do bioma todo.

Tendo em vista todas essas questões, nesta tese, respondemos a duas questões principais: (1) uma envolvendo a dinâmica espaço-temporal da estrutura da paisagem de todo o bioma da Mata Atlântica, e outra (2) em como estrutura da paisagem afeta as dimensões taxonômicas e funcionais de comunidades de anuros neste mesmo bioma. Relacionado a cada uma dessas questões, nós organizamos parte dos dados reunidos e tornamos os mesmos disponíveis para a toda a comunidade científica, por meio de dois data papers: (1) o primeiro com 500 rasters das informações de métricas de paisagem, topografia, hidrografia e antrópicas (ATLANTIC SPATIAL); e (2) o segundo com atributos funcionais morfológicos e ecológicos de parte da diversidade de anfíbios ao longo de toda a Mata Atlântica (ATLANTIC AMPHIBIAN TRAITS).

Dessa forma, esta tese se estrutura em quatro capítulos:

Capítulo 1: *The Atlantic Forests of South America: spatiotemporal distribution of vegetation and implications for conservation*

Analisamos métricas de paisagem da vegetação florestal (VF), floresta e outras vegetações naturais (VN) e a sensibilidade das métricas a infraestruturas lineares (rodovias e ferrovias) entre 1986 e 2020 para toda a Mata Atlântica. Em 2020, os remanescentes de Mata Atlântica compreendiam 22,9% de VF e 36,3% de VN, extensão que diminuiu 2,4% e 3,6% desde 1986, respectivamente. As infraestruturas lineares afetaram principalmente os maiores fragmentos (>500.000 ha), reduzindo o seu tamanho entre 56% e 94%. O período anterior a 2005 foi caracterizado por perda de VN e VN (3% e 3,43%) e diminuição do número de fragmentos de VF e VN (8,6% e 8,1%). Em contrapartida, após 2005, a vegetação se estabilizou, com recuperação de cerca de 1 Mha de VF (0,6%) e aumento no número de fragmentos, em parte devido a políticas ambientais. Contudo, a Mata Atlântica ainda é um domínio altamente fragmentado: 97% dos fragmentos de vegetação são pequenos (<50 ha), com tamanho médio de fragmento entre 16,3 e 25,5 ha; 50-60% da vegetação está a <90 m de suas bordas, e o isolamento entre os fragmentos é alto (250-830 m). As áreas protegidas e territórios indígenas cobrem apenas 10% da vegetação da Mata Atlântica, e a maioria da vegetação se estende por mais de 10 km nessas áreas. Nosso trabalho destaca a importância da legislação e da análise da dinâmica da paisagem para auxiliar nos futuros programas de conservação e restauração da biodiversidade na Mata Atlântica.

Capítulo 2: *ATLANTIC SPATIAL: a data set of landscape, topographic, hydrological, and anthropic metrics for the Atlantic Forests of South America*

Disponibilizamos um conjunto de dados de informações geoespaciais integradas e em escala precisa (resolução = 30 m) para toda a extensão da Mata Atlântica para o ano de 2020. Esse conjunto de dados é composto por 500 rasters com métricas de paisagem, topografia, hidrografia e antrópicas, e por um vetor de polígono de delimitação da Mata Atlântica, disponível através do pacote R atlanticr (https://mauriciovancine.github.io/atlanticr), que desenvolvemos para facilitar a organização e aquisição dos dados. Esse conjunto de dados permite a integração eficiente de dados ambientais e de biodiversidade para a Mata Atlântica em futuros estudos ecológicos, e esperamos que sejam uma importante referência e fonte de

dados para planejamento da paisagem, conservação da biodiversidade e programas de restauração florestal.

Capítulo 3: *Landscape structure as the predictor of anuran taxonomic and functional diversity in a highly threatened hotspot*

Avaliamos o efeito da estrutura da paisagem na diversidade taxonômica e funcional de anuros na Mata Atlântica brasileira. Nossa hipótese foi de que a desconexão de habitat (descontinuidade entre habitat terrestres e aquáticos) seria o principal preditor das medidas de diversidade de anuros. Utilizamos 324 comunidades com 274 espécies de anuros e 12 atributos funcionais para medir a diversidade taxonômica (número de espécies com reprodução aquática e reprodução terrestre) e diversidade funcional (riqueza, regularidade e divergência funcional). Nossos resultados mostraram que a perda de habitat foi o principal preditor da diversidade taxonômica e funcional, embora a desconexão do habitat também tenha sido importante para pelo menos um dos componentes da diversidade funcional. Concluímos que a quantidade de habitat florestal, assim como a quantidade de habitat aquático e a manutenção da conexão entre ambos são fundamentais para a manter múltiplos aspectos da diversidade de anuros na Mata Atlântica.

Capítulo 4: *ATLANTIC AMPHIBIAN TRAITS: a data set of morphological and ecological traits of amphibians in the Atlantic Forest*

Reunimos um conjunto de dados que inclui características morfológicas e ecológicas tanto ao nível individual quanto de espécie. No nível individual, medimos 2.489 indivíduos representando 357 espécies de anuros em 17 famílias (50% da diversidade de anfíbios da FA), provenientes de espécimes da coleção herpetológica CFBH (Célio Fernando Baptista Haddad). Medimos 12 características morfológicas contínuas, incluindo tamanho do corpo, formato da cabeça e membros locomotores relevantes para características de história natural, alimentação, níveis tróficos, locomoção, migração e dispersão. O conjunto de dados ao nível de espécie compreende 17 características ecológicas (relacionadas ao habitat, reprodução e características tróficas) de 533 espécies de anfíbios em 21 famílias (74% da diversidade de anfíbios da AF). Este conjunto de dados é um recurso valioso para o avanço das pesquisas sobre os impactos antrópicos e das alterações climáticas na diversidade funcional dos anfíbios nos ecossistemas da Mata Atlântica.

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CAPÍTULO 1: The Atlantic Forests of South America: spatiotemporal distribution of vegetation and implications for conservation

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The Atlantic Forest of South America: spatiotemporal dynamics of the vegetation and implications for conservation

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Highlights

- There is 23% forest and 36% natural vegetation cover in the Atlantic Forest.
- Between 1986 and 2020, native forest cover decreased by 2.4% and natural vegetation by 3.6%.
- Since 2005, there has been a 1 Mha increase in forest area by small fragments (1 ha).
- Roads and railways subdivide the largest vegetation fragments (>500,000 ha), reducing their size by 56%–94%.
- Alarmingly, 97% of fragments are small (<50 ha) and 50–60% of the vegetation is <90 m from its edges.

Abstract

The Atlantic Forest in South America (AF) is one of the world's most diverse and threatened biodiversity hotspots. We present a comprehensive spatiotemporal analysis of 34 years of AF landscape change between 1986 and 2020. We analyzed landscape metrics of forest vegetation only (FV), forest plus other natural vegetation (NV), and the sensitivity of metrics to linear infrastructure. Currently, the AF remnants comprise 22.9% of FV and 36.3% of NV, an extent that has decreased by 2.4% and 3.6% since 1986, respectively. Linear infrastructure affected mainly the largest fragments (>500,000 ha), reducing their size by 56%–94%. The period before 2005 was characterized by loss of FV and NV (3% and 3.43%) and decrease in the number of FV and NV fragments (8.6% and 8.1%). In contrast, after 2005 the vegetation stabilized, with a recovery of 1 Mha of FV (0.6%) and an increase in the number of fragments, due in part to environmental policies. However, the AF is still a highly fragmented domain: 97% of the vegetation fragments are small (<50 ha), with an average fragment size between 16.3 and 25.5 ha; 50–60% of the vegetation is <90 m from its edges, and the isolation between fragments is high (250–830 m). Protected areas and indigenous territories cover only 10% of the AF vegetation, and most vegetation lies are >10 km in these areas. Our work highlights the importance of legislation and analysis of landscape dynamics to help future conservation and restoration programs for biodiversity in the Atlantic Forest.

Keywords: Landscape structure; Habitat loss; Habitat fragmentation; Edge effect; Isolation; Connectivity.

1 Introduction

Habitat loss, fragmentation, and degradation caused by human-induced changes are identified as the main drivers of biodiversity loss worldwide (Chase et al., 2020). The accelerated land use conversion resulting from these changes has affected especially forest ecosystems, causing a decrease in fragment size and an increase in edge effects (Fischer et al., 2021; Hansen et al., 2020). In recent decades, tropical and subtropical regions have lost >100 million hectares (Mha) of natural forests due to anthropogenic activities (Zalles et al., 2021). Despite the large impacts, few studies presented a spatiotemporal panorama long enough to describe and analyze changes in the landscape structure dynamics, especially in the Americas, where one of the most diverse and threatened biodiversity hotspot in the world is located: the Atlantic Forest in South America (AF) (Sloan et al., 2014).

The AF covers almost all the coast of Brazil and portions of Paraguay and Argentina, the three countries with the largest deforestation areas in the world between 1982 and 2016 (Song et al., 2018). Before European colonization, its vegetation covered over 1.6 million km^2 (Marques et al., 2021). Due to its high environmental heterogeneity, topographic variability, and pre-historic process of formation, the AF has high species diversity and endemism (Peres et al., 2020). With >18,000 species of plants (Flora e Funga do Brasil, 2023) and 3,500 species of vertebrates (Figueiredo et al., 2021; Reis et al., 2016), >65% of all (and 82% of the endemic) tree species are classified as threatened (de Lima et al., 2024). Additionally, the AF provides ecosystem services for >150 million people, such as water provisioning, hydroelectric energy generation, food production, pollination, soil protection, climate regulation, carbon storage, air quality, and cultural services (Joly et al., 2014).

An intensified degradation of the AF arises with the Portuguese colonization and the establishment of agricultural processes such as large plantation systems (sugarcane and coffee), extensive cattle production, energy demand (charcoal), fires, mining, and urban and industrial growth (Solórzano et al., 2021). These landscape modifications have affected the biodiversity in the AF for different taxonomic groups (Püttker et al., 2020) and ecological processes, such as seed dispersal (Marjakangas et al., 2020), carbon storage (de Lima et al., 2020), pollination (Varassin et al., 2021), and top-down regulation through top predators (Paviolo et al., 2016). Furthermore, other processes pose risks to the landscapes within the AF, such as defaunation (Galetti et al., 2021) and climate change (Vale et al., 2021). More recently, however, conservation actions have reduced deforestation rates and increased natural

regeneration, especially the Brazilian legislation (Federal Decree No. 750/93 and Atlantic Forest Law No. 11,428/2006) (Piffer et al., 2022b).

Despite the recent changes on the AF, few studies have analyzed the landscape structure in a space-time context on large time scales. In the most comprehensive study to our knowledge, Ribeiro et al. (2009) showed that only 11–16% of the forest cover remained in 2005, 83% of which was concentrated on isolated fragments smaller than 50 ha, and half of all forests were <100 m from their edges. Additionally, Tabarelli et al. (2010) and Ribeiro et al. (2011) showed a large proportion of forests remained in high elevations (>1600 m). Based on finer scale satellite data (5 m-spatial resolution), Rezende et al. (2018) estimated 28% of AF vegetation. In more recent studies, using data from MapBiomas (Souza et al., 2020), Bicudo da Silva et al. (2020) showed that landscape composition did not change substantially between 1985 and 2018, and that the loss in areas of montane vegetation was smaller than at lower elevations. In addition, Rosa et al. (2021) showed that the relative temporal stability of AF native forest cover (28 Mha) in recent years, was in fact due to the replacement of old-growth native forests in flatter terrains by young forests in marginal agricultural areas, resulting in increased isolation between forest fragments.

Even with these studies, there is a demand for a refined understanding of how landscape structure varied over time in the AF. Currently, Brazilian initiatives such as MapBiomas have been mapping land use and land cover change with wide thematic coverage, high spatiotemporal resolution, and standardized classification (Souza et al., 2020). This allows for the calculation and comparison of landscape metrics for large territorial extensions and time periods to understand the landscape dynamics of entire domains (Bicudo da Silva et al., 2020; Rosa et al., 2021). Moreover, the AF has a high density of linear infrastructure (e.g. roads, railways, power transmission lines and oil and gas pipelines) because of its high (and increasing) human population and industrial development, and the main large-scale effect on landscape configuration is related to roads and railways. These linear infrastructures severely impact natural vegetation connectivity and biodiversity (e.g. through deforestation, noise disturbance, pollution, and animal roadkill) (Cassimiro et al., 2023; Martinez Pardo et al., 2023), but have never been analyzed in the context of the landscape structure.

Here, we analyzed the spatiotemporal dynamics of the landscape structure of vegetation in the Atlantic Forest every five years from 1986 to 2020. To accomplish this large-scale evaluation, we used a wide delimitation of the Atlantic Forest, including Brazil, Argentina, and Paraguay. We accounted for forest vegetation types only (FV) and forest plus other natural vegetation types (NV) and quantified, in addition, the effect of linear

infrastructure on the AF landscape metrics. To understand the spatiotemporal landscape structure vegetation dynamics, we calculated the following landscape metrics for all FV and NV fragments in the AF domain: habitat amount, fragment size, number of fragments, fragment temporal dynamic, edge area, functional connectivity, isolation between fragments and distance from protected areas (PA) and indigenous territories (IT). These metrics were generated through an approach that allows for ecological interpretation of the influence of the landscape structure on organisms by accounting for species mobility, gap-crossing abilities, and sensitivity to edge effects (Riva and Nielsen, 2020).

2 Methods

2.1 Study region

AF extends from 3ºS to 33ºS, and from 35ºW to 58ºW with about 163 Mha, covering large coastal and inland portions of Brazil, Argentina, and Paraguay (Marques et al., 2021) (Fig. S1a). Due to its wide extent, the AF boundaries create important ecotones with other vegetation domains such as Cerrado, Caatinga, Chaco and Pampa (Marques et al., 2021). The vegetation from AF is a complex mosaic, mainly composed of five forest vegetation types—Dense Ombrophilous, Open Ombrophilous, Mixed Ombrophilous, Semideciduous Seasonal, and Deciduous Seasonal (Joly et al., 2014). Additionally, the AF also includes mangroves and coastal scrub vegetation (Marques et al., 2021). There are also many marginal habitats such as altitude grasslands (*campos rupestres* and *campos de altitude*), oceanic islands, beaches, rocky shores, dunes, marshes, inland swamps, and mountain forest (*brejos de altitude*) in the Northeast region (Scarano, 2002). To provide a broad picture in ecological and evolutionary terms, we used an integrative delimitation adapted from Muylaert et al. (2018), which encompasses the main proposed delimitations across several associated ecosystems. This delimitation was produced by overlapping available AF delimitations (Fig. S1[b-e] and Table S1) and adjusting the delimitation in the Eastern coastal areas using the Brazilian territorial delimitation from IBGE (https://www.ibge.gov.br) for 2021 (IBGE, 2021). This step ensures that areas of coastal vegetation such as mangroves, dunes, and wooded sandbank/sandy coastal plain vegetation (hereafter *restinga*) (Scarano, 2002) are better represented. The final delimitation has a total area of 162,742,129 ha, distributed within 3653 municipalities from 18 Brazilian states (93.1%), 70 municipalities of one province in Argentina (1.6%), and 127 municipalities from 11 departments in Paraguay (5.3%) (Fig. S1a, Fig. 3).

2.2 Mapping

We compiled land use and land cover maps for Brazil, Argentina, and Paraguay from MapBiomas Brazil collection 7 (https://mapbiomas.org) and MapBiomas Bosque Atlántico collection 2 (https://bosqueatlantico.mapbiomas.org) (Souza et al., 2020). These datasets reconstruct annual land use and land cover information at 30-m spatial resolution from 1985 to 2021, based on a pixel-based random forest classifier of Landsat satellite images using Google Earth Engine, with AF general accuracy of 89.8% (Souza et al., 2020). We used data for every fifth year between 1986 and 2020. We excluded the years 1985 and 2021 because there was no validation for the previous and subsequent year, respectively. We defined two groups of vegetation classes to convert the maps into non-vegetation/vegetation (0/1) binary rasters for landscape analyses. The first comprises only forest vegetation types ("Forest Vegetation", FV), which included the classes Forest Formation, Mangrove and Wooded Sandbank Vegetation (*restinga*). The second group of vegetation classes considered both forests and other natural vegetation types ("Natural Vegetation", NV), including Forest Formation, Mangrove, Wooded Sandbank Vegetation (*restinga*), Savanna Formation, Wetland, Grassland, Salt Flat, Herbaceous Sandbank Vegetation and Other Non-Forest Formations (Fig. S2a-h and Table S2).

We used roads and railways (for the year 2021 in Brazil and Argentina, and for 2012 in Paraguay) to trim their overlapping FV and NV fragments (henceforth called "trimmed" and "not trimmed" scenarios) (Fig. S11). This procedure enabled us to avoid overestimating the size of large fragments of vegetation and check the metrics' sensitivity to linear infrastructure (following Antongiovanni et al., 2018), since these structures might subdivide entire fragments, decrease landscape connectivity, and threaten multiple taxonomic groups (Cassimiro et al., 2023). Therefore, we analyzed four vegetation maps: "FV not trimmed", "FV trimmed", "NV not trimmed", and "NV trimmed". Further, we analyzed the overlap between FV and NV fragments with Protected Areas (PA; for the year 2022) and Indigenous Territories (IT; for the year 2021) (Fig. S12). Details of road, railway, PA, and IT maps are presented in the Data section in the Supplementary Material (Fig. S11 and Fig. S12). All geospatial datasets were rasterized and warped to 30 m-spatial resolution (112663 × 83307 ≈ 9.4 billion cells and ca. 1.8 billion cells with values) using the Albers Conical Equal Area Brazil (SIRGAS 2000) projection (https://spatialreference.org/ref/sr-org/albers-conical-equal-

area-brazil-sirgas-2000). International map displays were generated using Natural Earth (1:10,000,000) data and QGIS 3.22 LTR (QGIS Development Team, 2023).

2.3 Landscape metrics

All landscape metrics were processed in GRASS GIS 8.2.1 (Neteler et al., 2012) through the R 4.3.0 (R Core Team, 2023), using the *rgrass* package (Bivand, 2022), implemented on the LSMetrics package (Niebuhr et al. *in prep.*). We calculated six landscape metrics: number of fragments, fragment size, edge area, isolation, functional connectivity, and distance from PA and IT (Figure S13 and Table S3). The number of fragments and fragment size allowed us to account for the number and area of vegetation fragments for different size classes (Table S3). Fragments were defined using the eight-neighbor rule (Queen's case), which defines areas connected to pixels in eight directions (Turner and Gardner, 2015). We also examined the area and number of fragments that appeared and disappeared throughout time, and the areas of increase, reduction, and stability of fragments that remained in the landscape (Table S3) (Rosa et al., 2021). Edge area was calculated for different edge depths (distance from the edge of the fragment) (Table S3), allowing us to assess the amount and percentage of forest area subjected to edge effects (Harper and Macdonald, 2011).

Two metrics of functional connectivity were computed for different gap-crossing distances (species' capacities to cross non-habitat) (Table S3). First, we calculated the sum of the areas of all fragments closer than the gap-crossing distance, which can be interpreted as the functional available area of each clump of fragments (Awade and Metzger, 2008) or the amount of functional (i.e. suitable and well-connected) habitat (van Moorter et al., 2023). Second, we computed the expected cluster size as the mean fragment clump size, and then compared it with the highest cluster size in the entire study region. Isolation was calculated using an index adapted from the "*Empty Space Function*" (Dale and Fortin, 2014), similar to Ribeiro et al. (2009): we computed a Euclidean distance map from all the fragments, extracted its values and calculated the mean. We repeated this process by removing different-sized fragments in several steps (see Table S3 for classes of distance), and then created new Euclidean distance maps to recompute the mean distance values. These values represented the isolation of fragments while also providing insights about the importance of the smaller fragments (*stepping stones*) (Diniz et al., 2021). We calculated the amount of FV, NV, and vegetation classes (see Table S2) covered by PA and IT, and the shortest Euclidean distance from each FV and NV pixel to these areas (see Table S3 for classes of distance).

3 Results

3.1 Forest and natural vegetation cover

The proportion of the Atlantic Forest domain covered by forests and natural vegetation decreased in the past 34 years, from 25.26% (41.1 Mha) to 22.86% (37.2 Mha) for FV and from 39.86% (64.8 Mha) to 36.27% (59 Mha) for NV (Fig. 1 and Table S4). For the entire period, in Brazil the percentages decreased from 22.85% (34.6 Mha) to 22.27% (33.7 Mha) for FV and from 37.34% (56.5 Mha) to 35.25% (53.4 Mha) for NV, with an increase in the proportion since 2005 (Fig. S3). NV was mainly composed of savannas, grasslands, and wetlands, besides the forest formations. In Argentina, the loss of vegetation cover was proportionately larger, from 67.36% (1.8 Mha) to 56.89% (1.52 Mha) for FV, and 67.96% (1.81 Mha) to 57.33% (1.53 Mha) for NV, showing an increase in the rate of deforestation in the last five years (Fig. S3). In Paraguay, the loss of vegetation cover was higher than in the other countries, dropping from 54.57% (4.7 Mha) to 22.85% (2 Mha) for FV, and 75.26% (6.5 Mha) to 47.74% (4.1 Mha) for NV (Fig. S3), but it has remained relatively stable since 2005.

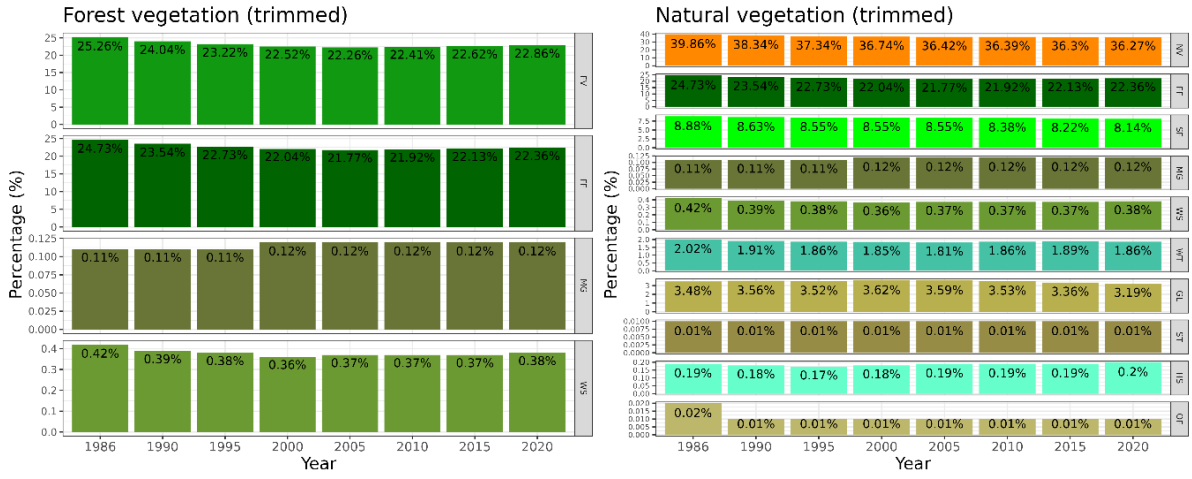

Figure 1. Vegetation cover for Forest Vegetation (FV) and Natural Vegetation (NV) through the years for the whole Atlantic Forest limit, trimmed by roads and railways. Abbreviations: Forest Formation (FF), Mangrove (MG), Wooded Sandbank Vegetation (*restinga*) (WS), Savanna Formation (SF), Wetland (WT), Grassland (GL), Salt Flat (ST), Herbaceous Sandbank Vegetation (HS), Other Non-Forest Formations (OF).

Beyond presenting the percentages for the integrative delimitation (Fig. S1a), we also present results for five other delimitations (Table S5). The results for 2020 (Fig. S1[b-f]) varied for FV from 23.15% (31.6 Mha) for the delimitation of Da Silva and Casteleti (2003) to 26.47% (29.3 Mha) for the delimitation of IBGE (2019), all trimmed by roads and railways. For NV, the results ranging from 31.45% (34.8 Mha) for the IBGE (2019) trimmed to 37.04% (40.9 Mha) for the delimitation of the Dinerstein et al. (2017) not trimmed (Table S5).

3.2 Number of fragments and fragment size distribution

Roads and railways greatly impacted the large-sized fragments, depending on the year and the scenario considered. These effects were mainly reflected in vegetation fragments larger than 500,000 ha, which reduced the maximum fragment size by 56%–94% (Fig. 2, Fig. S4, and Table S4). By accounting for linear infrastructure, the fragment size classes >500,000 ha ceased to exist for FV for all years and were heavily reduced for NV, and the total area and number of fragments increased for fragments of all size classes <500,000 ha for FV and NV (Fig. 2, Fig. 3, and Fig. S4). Despite this effect for large fragments, our results showed no difference between the scenarios “trimmed” and “not trimmed” for other landscape metrics. Therefore, we henceforth chose to demonstrate the results with the linear infrastructure effect (trimmed scenario) in the main text and present the additional results in the Supplementary Material.

For the trimmed scenario, about 97% of the fragments have an area of <50 ha, with 0.4% of variation over the years. However, between 1986 and 2020 the total area covered by these small fragments increased from 18.8% to 22.2% for FV and from 11.7% to 13.5% for NV (Fig. 2 and Fig. S4). For fragments between 50 ha and 25,000 ha, the proportion of the total number of fragments is low (2.5%), varying non-linearly for FV from 2.44% in 1986 to 2.61% in 2020; and for NV with 2.34% in 1986 to 2.61% in 2020. However, total area covered by fragments of this size class increased from 1986 to 2020, going from 40% to 46.1% for FV, and from 29.8% to 35.1% for NV (Fig. 2 and Fig. S4). For the last set of categories of fragment area, above 25,000 ha, we found a very small proportion of number of fragments (0.001%), with values falling from 0.0082% to 0.0061% for FV, and from 0.0127% to 0.0118% for NV, between 1986 and 2020. Total area values for FV fragments in these categories fell from 41.1% to 31.9% and for NV from 58.6% to 51.3%, between 1986 and 2020 (Fig. 2 and Fig. S4).

In 1986, the largest FV fragments were located in the coast of Bahia (*South of Bahia—cabruca region*), São Paulo, Paraná, and Santa Catarina (*Serra do Mar region*), and inland areas of Paraná, Santa Catarina and Rio Grande do Sul in Brazil. For the same period, there were large FV fragments in Misiones in Argentina and the eastern portion of Paraguay (Fig. 3a). We observed the same for NV, with additions of huge fragments in portions of Bahia, Minas Gerais, and Piauí in Brazil, mainly in the regions named *São Francisco* and *Brejos Nordestinos* (see these region concepts in Ribeiro et al., 2009) (Fig. 3c). In 2020, these same regions concentrated the largest fragments of FV and NV, but with a decrease in their area (Fig. 3[b-d]). The exception was Paraguay, where there was a vast deforestation process, mainly for FV (Fig. 3[c-d]). Our results also show a large effect of roads and railways on maximum fragment size, for the same regions (compare Fig. 3[a-d] with Fig. S5[a-d]).

The spatial-temporal analysis revealed a turning point for the AF landscape structure in 2005. For the first period (1986–2005), the number of fragments decreased by 8.6% for FV and 8.1% for NV; for the second one (2005–2020), it increased to 12.2% for FV and 9.3% for NV (Fig. 4a). From 2010 onwards, the number of FV and NV fragments tended to become more like each other (Fig. 4a). The average fragment size in the first period for FV dropped by 3.6% (18.4 to 17.8 ha) and remained stable for NV, dropping 0.5% (28.2 to 28 ha). In the second period, the FV had a larger drop of 8.5% for FV (17.8 to 16.3 ha) and 8.9% for NV (28 to 25.5 ha) (Fig. 4b).

The temporal dynamics of the landscape from 1986 to 2005 revealed a reduction in the total area of 4.87 Mha of FV (3%) and 5.56 Mha of NV (3.4%) (Table S6). However, between 2005 and 2020, there was an increase of 990,000 ha of FV (0.6%) and a small decrease of 240,000 ha of NV (0.15%). Considering the balance of fragments gained and lost, in the first period there was a sharp drop in the number of fragments for FV (242,000) and NV (227,000), but in the second period there was an increase for FV (385,000) and NV (314,000). Between 1986 and 2005, the average size of lost FV and NV fragments (1.2 to 1.35 ha) was greater than the size of restored fragments (1.08 to 1.14 ha); between 2005 and 2020, this pattern reversed, with the average size of fragments lost being smaller (0.94 to 0.97 ha) than that of fragments gained (1.03 to 1.08 ha).

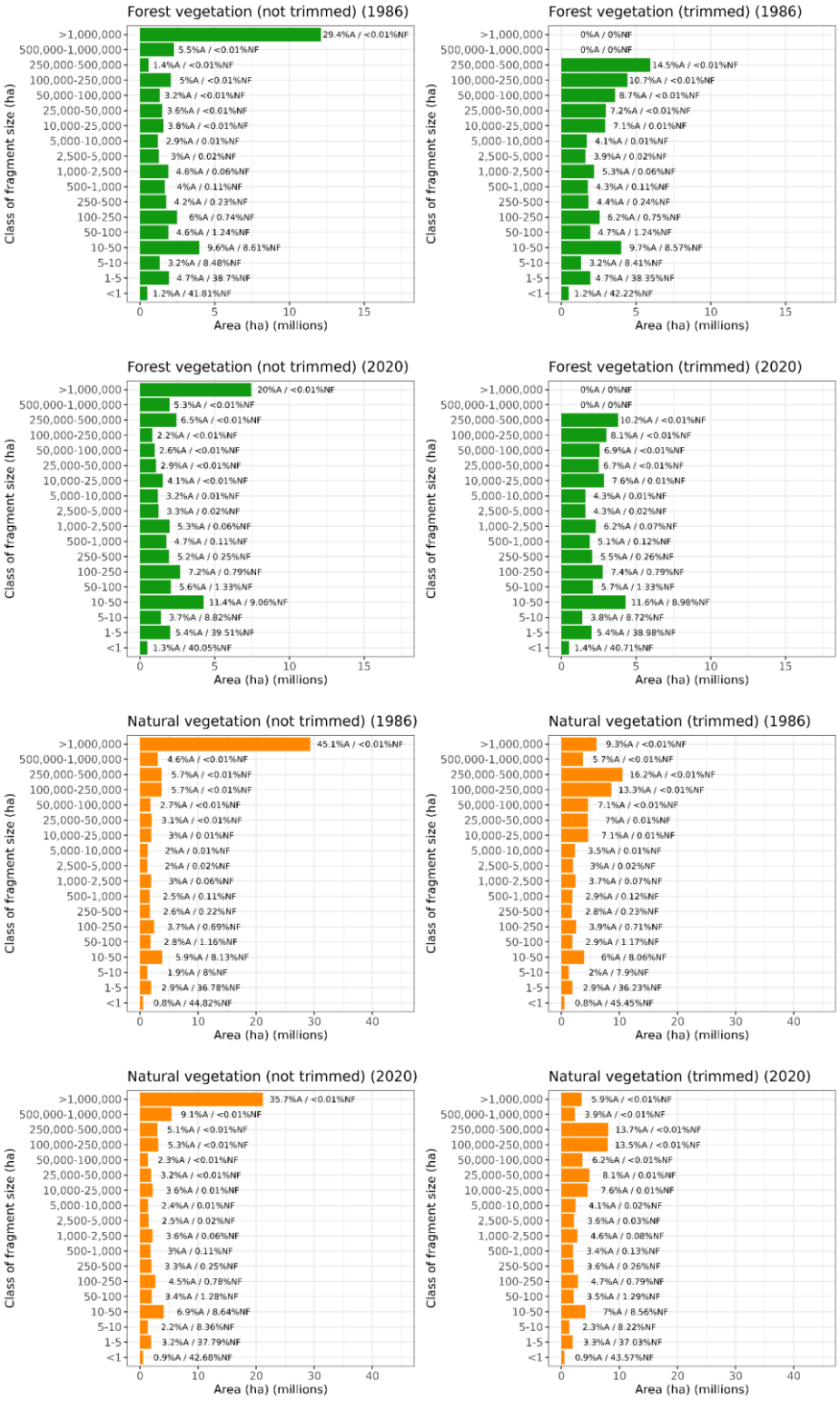

Figure 2. Distribution of Forest Vegetation (FV) and Natural Vegetation (NV) fragment sizes across the AF (1986 and 2020), trimmed and not trimmed by linear infrastructure. %A: percentage of the total area; %NF: percentage of the number of fragments. See Fig. 3S for other years (1990–2015). Please note the difference scales in the x-axis between the FV and NV plots.

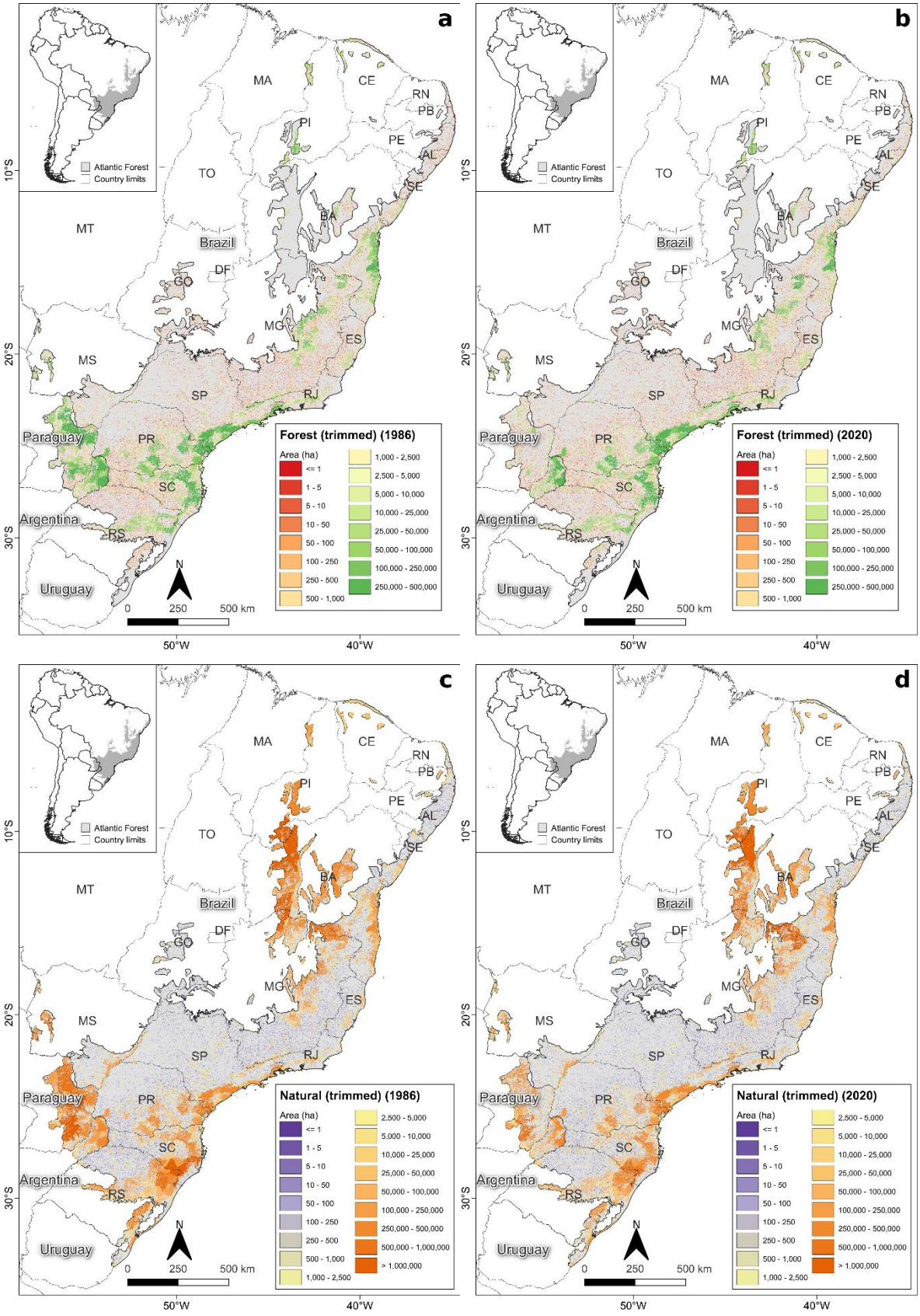

Figure 3. Fragment area for Forest Vegetation (FV) in 1986 (a) and 2020 (b), and for Natural Vegetation (NV) in 1986 (c) and 2020 (d), trimmed by roads and railways for the entire AF.

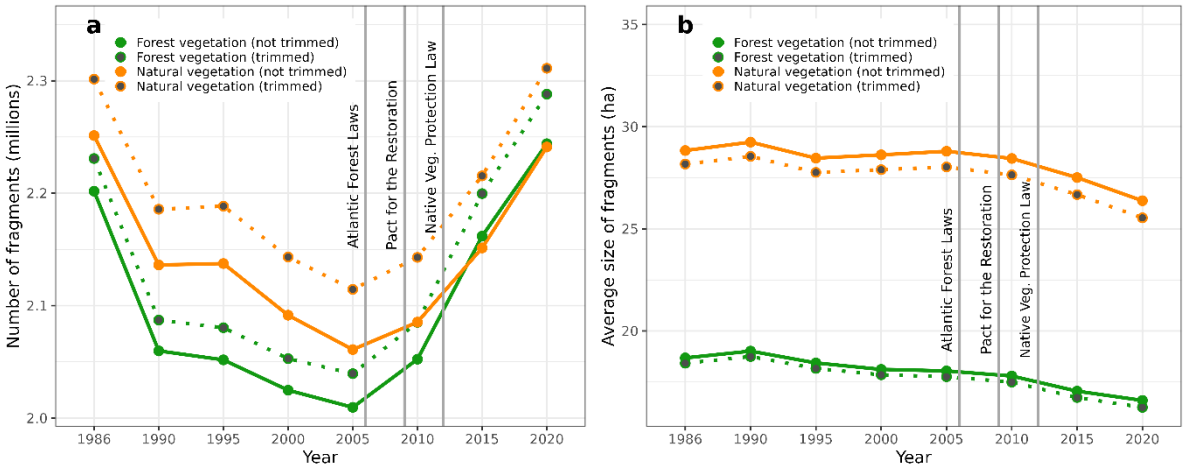

Figure 4. Distribution of (a) number of fragments and (b) average fragment sizes of Forest Vegetation (FV) and Natural Vegetation (NV) across the AF from 1986 to 2020, trimmed and not trimmed by roads and railways. The gray lines represent reference years when important legislation and restoration programs were created in Brazil (See Discussion for details).

3.3 Core and edge area

The percentage of FV and NV located <90 m from the edge increased over time, going from 51.9% to 58.8% for FV and 42.2% to 48.3% for NV, as well as the percentage <240 m, from 76% to 81.7% for FV and 66.2% to 72.2% for NV (Fig. 5[a-b]). Conversely, the amount of FV and NV located >500 m from any edge ("core areas") decreased, from 12.4% to 8.9% and from 19.5% to 15%, respectively. The maximum distances from fragment edges for FV and NV were substantially different— around 11 km for FV and 32 km for NV—showing that NV fragments have larger core areas (Fig. 5[a-b]). From 90 m onwards, there is an inversion in the edge percentage over time: between 1986 and 2020, there is a gradual increase in the percentage of vegetation <90 m; and a decrease in the percentage of vegetation >90 m from edges, showing a threshold for central areas of fragments into edge areas (Fig. 5[c-d]).

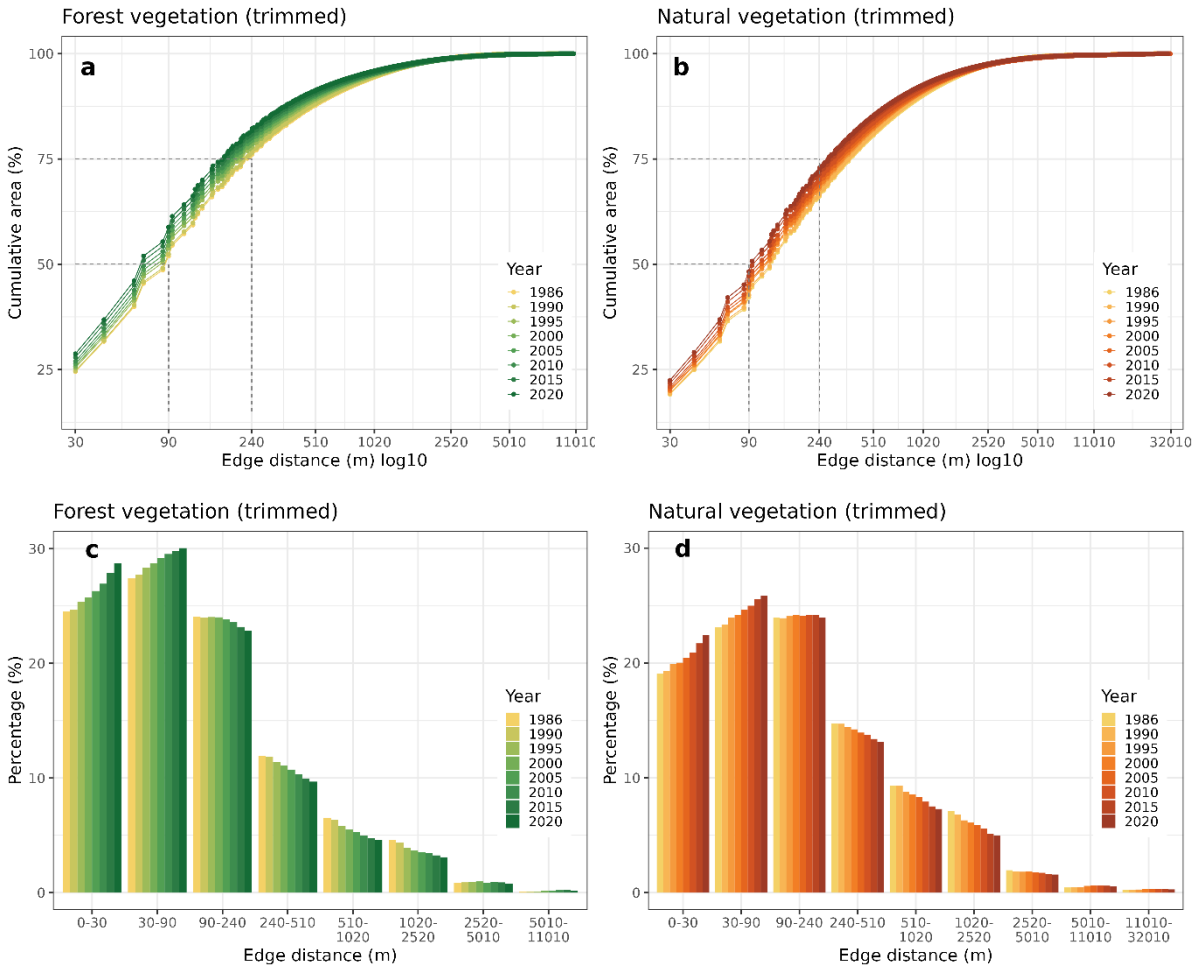

Figure 5. Cumulative (a and b) and per class (c and d) area under edge effect at different depths for the Forest Vegetation (FV) and Natural Vegetation (NV) in the AF trimmed by roads and railways. See Fig. S6 for not trimmed scenario.

3.4 Functional connectivity

The average functionally connected vegetation area—i.e. the vegetation area available and reachable for species—decreased for species with low-mobility in non-vegetation matrices (up to 60 m of gap-crossing) for both types of vegetation (decreasing 9.4% for FV and 6.5% for NV between 1986 and 2020, Fig. 6[a-b]). However, for species with high-mobility (gap-crossing above 120 m), the functional connectivity decreased until 2005 and then increased afterwards. The functional connectivity of the NV was always higher in numerical terms for the same years, but they followed the same patterns of annual trends and gap-crossing as the FV.

When we analyzed the largest functionally connected vegetation cluster, we noticed that species restricted to vegetation areas (gap-crossing = 0) have relatively small vegetation

area available (the largest fragments correspond to 1% of FV and 4% of NV cover, for all years, Fig. 6[c-d]). However, the area of the largest functionally connected cluster increases rapidly as species become more mobile, with the rate of increase varying largely between years and for species with different mobility. For high-mobility species (gap-crossing >600 m) the curve presenting the largest functionally connected cluster reaches an asymptote (representing 85% for FV and 72% for NV), and there is no increase in the largest functional patches even if species can move further into non-vegetation matrices. These patterns are similar for FV and NV.

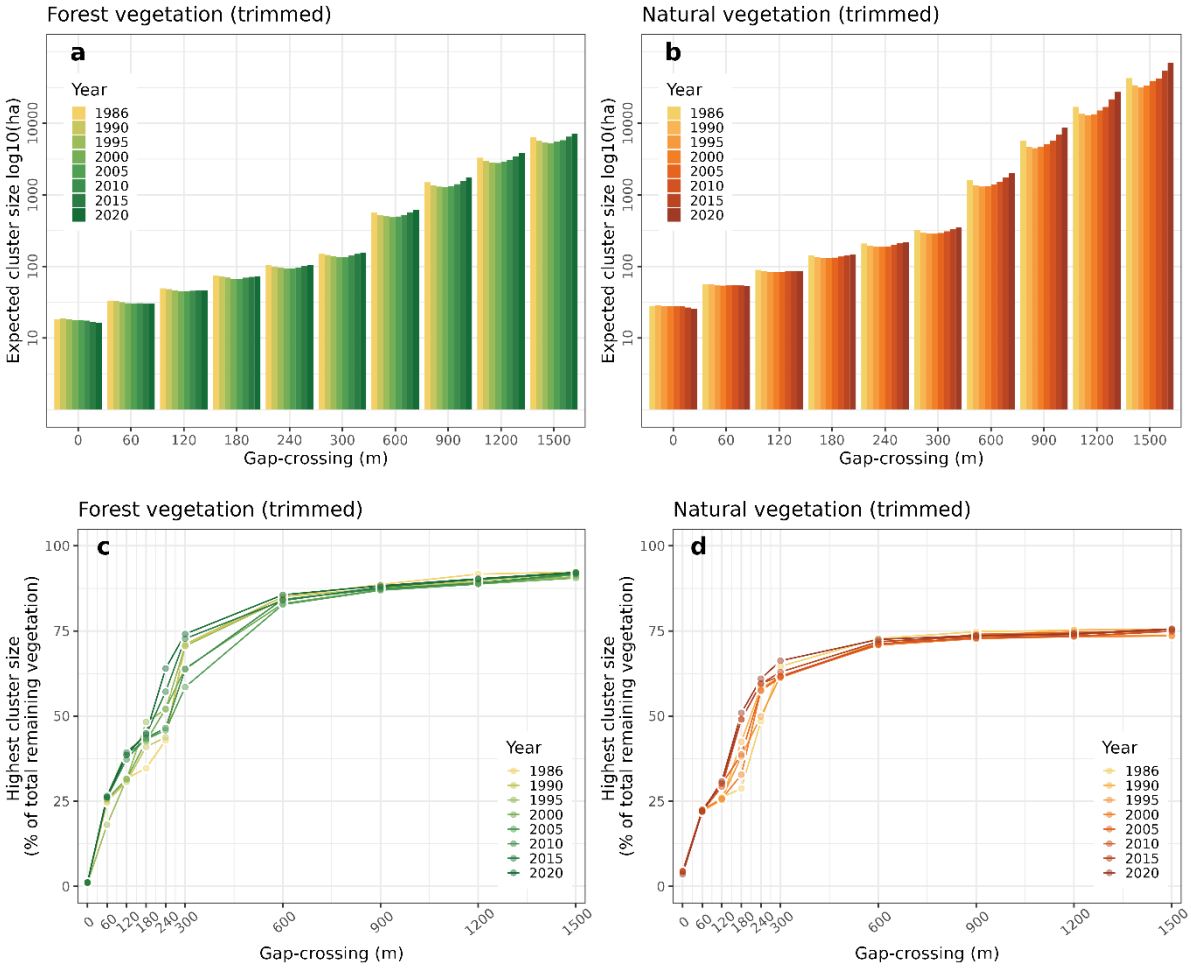

Figure 6. Expected cluster size (a-b) (average functional size; ha) of functionally connected fragments of Forest Vegetation (FV) and Natural Vegetation (NV) for different functional distance values (meters) for the AF trimmed by roads and railways. Highest functionally connected vegetation cluster (c-d) (% of total cover of FV and NV) estimated across varying functional distances (meters) for the AF. See Fig. S7 for not trimmed scenario.

3.5 Mean isolation

Small fragments were key to reducing isolation between fragments in all analyzed scenarios. For example, when we disregard fragments <50 ha, the mean isolation increases by 370–495% for FV and 351–444% NV (Fig. 7[a-b]). As we increase the size of fragments removed, there is a gradual increase in isolation, varying to 4-22 km for FV and 1-12 km for NV. Importantly, the mean isolation was reduced by 65–70% when considering that NV also connects forests and other NV fragments (Fig. 7[a-b], Fig. S8[a-b]). Considering the temporal trends, in 1986, the mean isolation for the entire AF region was 773 m for FV and 273 m for NV. The isolation reached its maximum values in 1995, after which, it slowly decreased until 2015, and more recently it fell to 832 m for FV and 253 m for NV in 2020 (Fig. 7[a-b]).

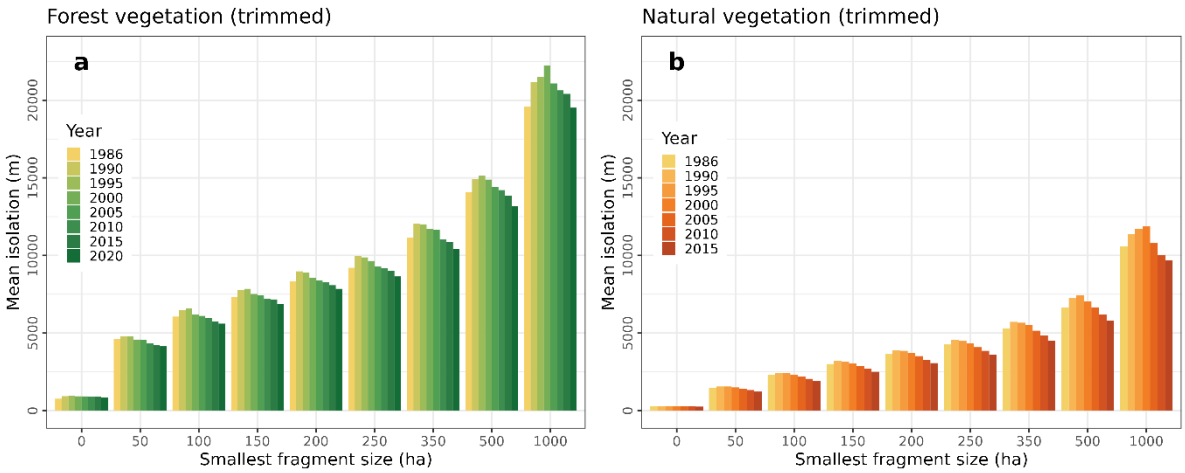

Figure 7. Mean isolation between fragments of Forest Vegetation (FV) and Natural Vegetation (NV) trimmed for the AF trimmed by roads and railways. Smallest fragments size: 0 ha (all fragments), 50 ha, 100 ha, 150 ha, 200 ha, 250 ha, 350 ha, 500 ha, and 1000 ha. See Fig. S8 for not trimmed scenario.

3.6 Protected areas and indigenous territories

Protected areas (PA) covered 4.6 Mha (2.84%) and indigenous territories (IT) covered 1.3 Mha (0.81%) of the AF limit. These values represent 12.4% and 7.8% of the total FV and NV area for PA, and 3.6% and 2.2% of the total FV and NV area for IT in 2020. However, only 3.1 Mha (8.4%) of FV and 4.1 Mha (7%) of NV cover overlaps with PA (Fig. 8[a-b]), and only 560,000 ha (1.5%) of FV and 760,000 ha (1.3%) of NV overlaps with IT (Fig. 8[c-d]), since other types of land cover occur within PA and IT. Only 2.7% of FV and 2.2% of NV

are within 1 km of PA and 0.8% of FV and 0.7% of NV to IT. For vegetation within 10 km, there are 23.4% of FV and 19.2% of NV of PA, and 9.5% of FV and 8.7% of NV of IT (Fig. 8). On the other hand, 68.2% of the FV and 73.9% of NV are over 10 km away from PA, and 89% of the FV and 90.2% of NV are over 10 km away from IT, demonstrating the lack of protection for these fragments of vegetation (Fig. 8).

The vegetation class with the largest area overlap is the Forest formation, with 3 Mha (8.2%) for PA and 536,000 ha (1.5%) for IT (Fig. S10). The classes with the largest proportional cover under protection are *restinga* with 133,000 ha (21.6%), Mangrove with 23,000 ha (11.9%), and Herbaceous sandbank vegetation with 31,000 ha (9.6%) (Fig. S10b). For IT, the class with the most cover proportion is the Other non-forest formations 1,400 ha (8.6%), followed by *restinga* with 22,000 ha (3.6%), and Mangrove with 4,600 ha (2.4%) (Fig. S10d). The Savanna formation class is the smallest cover protection with only 507,000 ha (3.8%) in PA (Fig. S10b) and 120,000 ha (0.9%) in IT (Fig. S10d), whose total area is second in terms of total area, 13 Mha (22.5%).

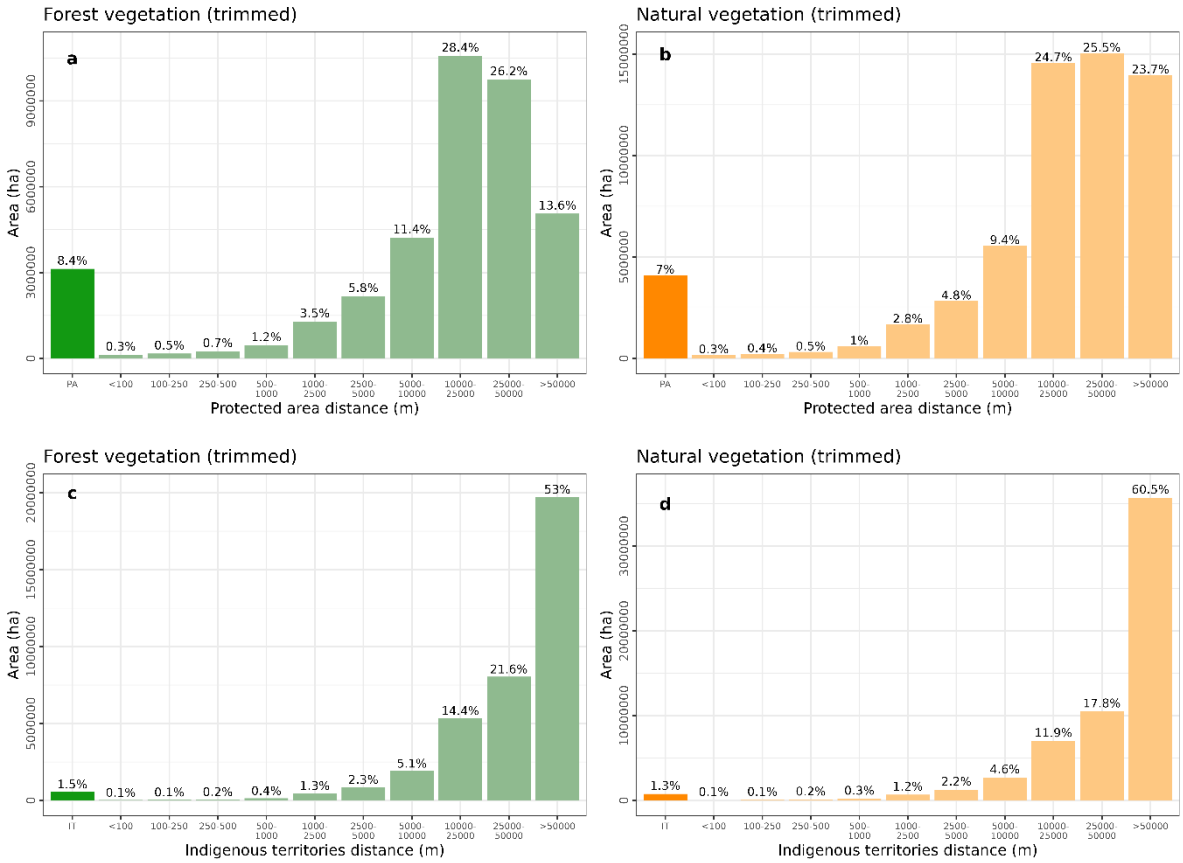

Figure 8. Amount of AF vegetation trimmed by roads and railways (area and percentage) and their distance (meters) from protected areas (PA; a – FV and b – NV) and indigenous territories (IT; c – FV and d – NV) per class. See Fig. S9 for not trimmed scenario.

4 Discussion

4.1 Main results

We present here a new panorama on the Atlantic Forest vegetation dynamics, by providing a comprehensive spatial and temporal analysis, integrating different types of vegetation, and considering for the first time the whole distribution of the AF, including Brazil, Argentina, and Paraguay. In the 34-year period analyzed, there was a substantial decrease in the vegetation cover in the AF, especially in Paraguay and Argentina and in Brazil until 2005. Within Brazil, and to a lesser extent in Argentina and Paraguay, we found a turning point for the Atlantic Forest around 2005. The period before 2005 was characterized by deforestation and decrease in the number of forest fragments; the period after 2005 was instead characterized by a larger stability in vegetation cover and an increase in the number of fragments. This result is linked, at least in part, to the environmental legislation in these countries (see Fig. 4 and next section for legislation details). Yet, there were marked changes in the spatiotemporal dynamics of the landscape structure for the entire AF, with an overall replacement of larger forest and vegetation areas by smaller fragments and vegetation areas increasingly subject to edge effects. Even with local and temporal changes, and although legislation, natural regeneration and small restoration actions appear to have positively affected them, the overall picture is still of a highly fragmented domain: a few vegetation fragments are very large, but >97% of the fragments are smaller than 50 ha, the mean fragment size decreased for both FV and NV, and more than half of the vegetation is closer than 90 m to edges with other land cover types.

Even though forest fragment sizes have decreased, we showed that the small fragments might still be very important for decreasing the isolation between forests and increasing the functional connectivity for medium- to high-mobile organisms. In this regard, we showed that non-forest natural vegetation is very important to increase connectivity between forests and between other non-forest natural vegetation fragments for organisms that can use them as suitable habitat or to move and reach suitable habitats. In contrast, species with low-mobility which are limited to forest fragments have seen a decrease in the available habitat area over time. We also showed that linear infrastructure such as roads and railways have a critical effect in fragmenting forests and natural vegetation, especially in the larger fragments. Importantly, there is only a small amount of forest and natural vegetation within the protected areas and indigenous territories, and most of the vegetation (70% for FV and

90% for NV) lies beyond 10 km from these areas. Below, we revisit these results to put them into context, and we explore key implications of our findings.

4.2 Forest and natural vegetation cover

Determining how much of the AF vegetation cover is left has always been a complex task. While we found 22.86% for FV and 36.27% for NV using an integrative AF delimitation in 2020, for the same year, the vegetation cover values varied from 23.15% to 37.04% for different delimitations and vegetation types. These values are smaller than the vegetation cover estimated in the Caatinga (50% in 2009; Antongiovanni et al., 2018), the Cerrado (54% in 2019; Pompeu et al., 2024) and the Brazilian Amazon (80% in 2021; Guedes Pinto et al., 2023). However, over the years, several studies have shown values ranging from 8% to 28% for different years for the AF (e.g. Bicudo da Silva et al., 2020; Da Silva and Casteleti, 2003; Rezende et al., 2018; Ribeiro et al., 2009). These estimates vary according to mapping resolution, size of vegetation fragments, types of vegetation (forest or non-forest), vegetation quality (primary or secondary forest), and AF delimitation (Ribeiro et al., 2009). We highlight that the use of MapBiomas mapping version 7, with image standards and classification methods, made the comparison of annual maps possible due to the decrease in random error between them (Souza et al., 2020). However, there are limitations associated with the methods used for mapping that are intrinsic from the database that we used. As an example, despite having a precise scale, MapBiomas does not clearly define vegetation successional stages and the quality of the forest remnants.

The vegetation cover showed a considerable decrease over time for Paraguay and Argentina, and a less pronounced decrease for Brazil, between 1986 and 2005. After 2005, the percentage of vegetation stabilized or increased, mainly in Brazil and for FV. These effects can at least partially be related to nature conservation laws (see Fig. 4 for some examples), which were initiated almost in the same period in Brazil (Atlantic Forest Law in 2006, and Native Vegetation Protection Law in 2012), Argentina (Forest Law in 2007), and Paraguay (The Zero Deforestation Law in 2004) (Silva et al., 2017; Dam et al., 2019). In Brazil, the AF Law has a clear effect on forest regeneration, as it reduces deforestation in advanced successional stages and requires that, when it occurs, it must be compensated, causing forests to emerge in secondary stages of regeneration (Piffer et al., 2022b). Besides, in Brazil, other specific conservation laws were established from 1988 on (Fauna Protection in 1988, and National System of Conservation Units in 2000), and more recently, the 2012 legislation

Natural Vegetation Protection National Law (Law 12.651/2012 – known as Forest Code – FC) created the Rural Environmental Registry [Cadastro Ambiental Rural (CAR)], which requires environmental information from private rural properties. CAR can be a fundamental tool to stimulate and regulate natural regeneration and direct vegetation restoration efforts through legal reserves (LR; in the Atlantic Forest it represents 20% of private land) and permanent preservation areas (PPA; riparian vegetation along stream and springs) (Brock et al., 2021; da Silva et al., 2023). Furthermore, since 2009, the Pact for the Restoration of the Atlantic Forest (AFPR; https://pactomataatlantica.org.br) has been encouraging restoration with the goal to restore 15 Mha by 2050 (Melo et al., 2013), with about 700,000 ha forest restored between 2011 and 2015 (Crouzeilles et al., 2019). Yet, Bicudo da Silva et al. (2023) showed that between 2001 and 2015 there was a process of forest transition in the AF, from forest cover loss to forest recovery (Rudel et al., 2005), due to the stagnation of agricultural activities and subsequent migration of small farmers to urban areas, the emergence of non-agricultural rural activities and the decrease in precipitation, which, together, led to the abandonment of land and favored natural regeneration.

In Argentina, the percentage of forest has been reduced linearly since the 1990s, with the combined effect of the advance of small-scale agriculture associated with population growth and road construction in some areas, and the increase of monospecific forest plantations incentivized by government subsidies and the participation of large timber companies (Izquierdo et al., 2008). The forest loss rate was lower during 20052–015, potentially because of the effect of the certified wood market in this region and the approval of the National Forest Law and the implementation of the National Fund for the Enrichment and Conservation of Native Forests (Fundación Vida Silvestre Argentina & WWF, 2017). However, forest loss increased in the last period (2015–2020) most likely due to higher levels of economic growth and the impact of long-term policies on the expansion of agriculture and cattle raising in Misiones (Mohebalian et al., 2022). Paraguay showed the highest rates of deforestation of the entire Atlantic Forest between 1986 and 2005 due to the massive expansion of agriculture. However, since the creation of the Zero Deforestation Law and the implementation of associated mechanisms, there has been a relative stabilization of vegetation loss (Da Ponte et al., 2017; Fundación Vida Silvestre Argentina & WWF, 2017).

While legislation and conservation instruments to protect forests and natural vegetation are essential to reduce habitat destruction, stimulate restoration and natural regeneration, they come with heavy social consequences, entering in conflicts with the rural life and work of peasants and traditional and indigenous groups that depend directly on the

forests (Sparovek et al., 2012; Gerhardt, 2016). Furthermore, a large part of the land in the AF is currently private or public land already subject to protection, which poses yet another challenge for future protection (Sparovek et al., 2019). Future research should investigate how spatiotemporal changes in landscape structure are linked to land tenure distribution, population migration to cities, and the social and cultural consequences of these processes. Melo et al. (2023) showed that restoration opportunities in the Caatinga should account for land concentration and socioeconomic contexts if one wants to avoid reproducing inequalities, what is also critical in the AF and should be a priority for future research and policies.

4.3 Number of fragments and fragment size distribution

Our analyses demonstrated that between 2005 and 2020 there was an increase in the amount, number of fragments, and higher mean fragment gain for forest vegetation, with new fragments appearing in previously deforested areas. This change illustrates in time a large-scale process which includes both natural forest regeneration (Crouzeilles et al., 2020) and forest transitions (Bicudo da Silva et al., 2023) related to other processes, and confirms the results found by Rosa et al. (2021), Piffer et al. (2022b) and Dias et al. (2023), who highlighted the replacement of older vegetation by younger vegetation in the AF. This replacement can lead to the loss of habitat quality in vegetation fragments, altering landscape features and affecting vital ecological processes and ecosystem functioning, such as carbon cycling (Piffer et al., 2022a) and vegetation structure (Faria et al., 2023).

We also found a large effect of roads and railways on fragment size, more pronounced in FV than in NV due to greater density of these linear infrastructures in large forest fragments located in Serra do Mar and southern Bahia in Brazil, and in the region of Misiones in Argentina. Roads and railways have a large impact on biodiversity, for example by modifying animal movement patterns, reducing connectivity between populations, and causing roadkills, which might lead to population declines and local extinctions (Cassimiro et al., 2023; Martinez Pardo et al., 2023). For example, almost 38 thousand mammal roadkills were estimated in 10 years in the state of São Paulo (which is covered almost entirely by Atlantic Forest vegetation), and an extrapolation of the analysis predicted 40 thousand roadkills per year only in the state of São Paulo (Abra et al., 2021).

When analyzing the distribution of fragment sizes, we noticed a reduction in the number and area of the fragments >500,000 ha of FV and NV between 1986 and 2020 and a clear increase in small fragments <50 ha. These results show a worrying pattern, much worse

than Ribeiro et al. (2009), and can be explained by the increase in mapping quality, with MapBiomas standardized approaches for mapping in detail vegetation fragments (including fragments <3 ha) that are considered secondary vegetation (Rosa et al., 2021). The increase in the proportion of smaller fragments has a direct impact on the maintenance of species diversity and population size of multiple taxonomic groups. Several studies have estimated fragment size and habitat amount thresholds for assemblage diversity in the AF, such as terrestrial mammals (Magioli et al., 2015), bats (Muylaert et al., 2016), birds (Barbosa et al., 2017), and multiple other groups (Banks-Leite et al., 2014).

However, since 97% of the fragments are <50 ha in the AF, the overall scenario is already well under the thresholds that are known to affect biodiversity persistence and composition (Banks-Leite et al., 2014; Magioli et al., 2015). In this context, approaches for conservation could be focused on single large *and* several small (SLASS) fragments (Szangolies et al., 2022). The SLASS approach can be more beneficial for conserving the AF biodiversity than choosing a unique type of conservation approach (SLOSS debate - single large or several small, see Fahrig et al. 2022). The current scenario is composed by a continuum of forest fragments within protected areas in the mountain range (Serra do Mar and Serra da Mantiqueira regions) and small remnants in the countryside mostly composed by riparian forest and legal reserves protected by law, added to hundreds of Private Reserves of Natural Heritage (RPPNs) to locally protecting endangered species (Rambaldi et al., 2005). Drastically changes in the vegetation configuration of the AF nowadays are highly unlikely since agricultural land, pasture and urban areas are already established in flatter terrains (Rosa et al., 2021). Therefore, the SLASS strategy could help to ensure that the vegetation in steeper terrain remains protected and increase the protection of riparian forests in flatter terrain.

4.4 Core and edge area

Our results showed that around 50% of the vegetation is up to 90 m, 75% of the vegetation is up to 240 m, and almost 90% of the vegetation is up to 500 m from the nearest edge (similar to Haddad et al. 2015), and may therefore be subjected to edge effects (de la Sancha et al., 2023; Parra-Sanchez and Banks-Leite, 2020; but see Harper et al., 2023). Over time, there was an increase in vegetation located closer than 90 m from the edges, revealing a possible edge effect threshold in the AF. Below this value, there is an intensification of edge effects, and above it, there is a decrease in the amount of vegetation core. This threshold is probably associated with the massive number and small average size of fragments we

detected. Importantly, small fragments are more subject to edge effects due to their size and shape (Fahrig, 2003). The edge effect changes the AF landscape features such as microclimate and carbon cycle (Magnago et al., 2015, 2017) depending on the fragment shape (Banks-Leite et al., 2013) and the matrix effect (Adorno et al., 2021). In that regard, numerous studies have demonstrated the negative effects of edge changes for epiphyte plants, small mammalian, and birds in the AF (de la Sancha et al., 2023; Morante-Filho et al., 2018; Parra-Sanchez and Banks-Leite, 2020). Despite this, Harper et al. (2023) showed that the edge effect for plant species did not exceed 20 m but recognizes its importance for conservation planning. Added to that, Pivello et al. (2021) and dos Santos et al. (2019) identified that AF is highly fire-sensitive, which changes the conditions of the edges and hinder natural regeneration. Some measures such as forested or agroforestry matrices and strips of trees being planted, forming a buffer around the existing fragments, can reduce the edge effect (Gama-Rodrigues et al., 2021; Tavares et al., 2019).

4.5 Functional connectivity and mean isolation

Functional connectivity and isolation had co-varying response patterns over time, with the lowest functional connectivity and highest isolation among fragments between 1990 and 2000, and from 2005 onwards there were clear signs of improvement, with increase of functional and decrease of isolation between vegetation fragments. The vegetation amount has not changed noticeably since 2005, and this improvement was due to the appearance of new fragments that increased the connectivity of the landscape, serving as stepping stones for mobile species. In this way, small fragments (<50 ha, which represents 97% of AF remnants) play a fundamental role in keeping large fragments connected, mainly for species that can cross non-vegetation matrices (Hatfield et al., 2018b; Diniz et al., 2021). Additionally, we have shown here that non-forest natural vegetation plays a key role in decreasing the isolation between forest fragments. Although there may be fewer forest-specialist species that use other types of vegetation, other natural vegetation types can be critical to maintaining AF connectivity for multiple species groups and ecological processes (Lyra-Jorge et al., 2010).

Our approach to evaluate connectivity and isolation focus on landscape structure, and when applied should be complemented by assessments of the permeability of the matrix between vegetation fragments (Hatfield et al., 2018a). Practices such as agroecology and forestry can increase the connectivity by increasing the permeability of the matrix for some groups of organisms (Tubenchlak et al., 2021). Furthermore, the AFPR and the CAR might be

a great opportunity for land use planning to create and improve ecological corridors (da Silva et al., 2023; Melo et al., 2013; Pinto et al., 2014). Finally, although connectivity and isolation were not sensitive to roads and railways, this lack of sensitivity appear due to short-distance divisions into FV or NV fragments, and to the fact that the additional cost that these linear infrastructures pose to animal movement and survival (Martinez Pardo et al., 2023) was not considered. Thus, management measures such as fauna passages might be fundamental for improving landscape permeability to maintain wildlife gene flow and reduce roadkill in landscapes highly fragmented by linear infrastructure such as the AF (Cassimiro et al., 2023; Teixeira et al., 2017, 2022).

4.6 Protected areas and indigenous territories

Alarmingly, we show that the proportion of total vegetation area formally protected by PAs (9.9% for FV and 8.3% for NV) is far below the targets of the post-2020 Global Biodiversity Framework (30% land surface by 2030, Jung et al., 2021). We highlight those indigenous territories, despite not being PA, have proven to be fundamental for forest restoration in the AF (Benzeev et al., 2023), but they only comprise 1.5% of FV and 1.3% of NV total area. Moreover, we found that most of the vegetation is located >10 km distant from PA and IT (70% for FV and 90% for NV). Our findings are consistent but more alarming than those found by Ribeiro et al. (2009) and Rezende et al. (2018). The Forest Formation class has the greatest overlap with PAs (8.2%) and IT (1.5%), given that forests are the main target for the creation of PAs and IT, and is the main class in the composition of the AF (62.1%). In addition, *restinga* and mangroves had a high overlap with PA and IT (40%), due to the high density of these protective measures on the Brazilian coast, especially in Serra do Mar. However, despite this high proportion of protection, these ecosystems have faced many threats in recent decades, which can affect several functions of ecosystems and local populations (Diniz et al., 2019). Savanna formation was critical to ensuring overall connectivity in the AF, but this class has the lowest proportion in PA and IT (4.7%) despite representing 23% of the amount of vegetation, possibly because this vegetation formation is not formally protected by specific AF protection laws. Since deforestation outside PA and IT has been lower than in private rural areas (da Silva et al., 2023), these areas are essential to ensure and promote biodiversity conservation (Avigliano et al., 2019; Benzeev et al., 2023). Therefore, it is necessary to create new protection instruments that focus on multiple types of natural vegetation, as well as strengthen the connection network between existing ones, and

that account for the surroundings of forested areas to promote the regeneration and restoration of vegetation.

4.7 Conservation implications and applications

The Atlantic Forest presented a panorama of greater effect of vegetation loss and fragmentation than other biomes such as the Caatinga (Antongiovanni et al., 2018), the Cerrado (Pompeu et al., 2024) and the Amazon (Lapola et al., 2023). Despite this, due to their long history of occupation and degradation, valuable conservation lessons can be applied to these biomes, mainly in relation to the abundance of restoration studies carried out in the Atlantic Forest (Guerra et al., 2020). Guedes Pinto et al. (2023) highlight governance lessons from the Atlantic Forest that can be applied in the Brazilian Amazon: (i) to create large protected areas for conserved areas in public lands, (ii) to create protected areas in the hotspots of deforestation in private lands [Reserves of Natural Heritage (RPPN)], (iii) to create a specific legislation for the biome (such as AF Law) in addition to the FC, (iv) forest restoration of LR and PPA in accordance with the FC, and (v) ensure natural regeneration and stimulate it through mechanisms such as payment for ecosystem services. The authors also point out that the main lesson is regarding the urgency of these measures, given the context of climate crisis and ecosystem services, the formulation and implementation of these measures must be adopted urgently in the Amazon, unlike the Atlantic Forest. Similar measures can be adapted and applied to other biomes, such as Cerrado and Caatinga, which despite having less vegetation remnants than Amazon, can benefit from conservation lessons learned and implemented in the Atlantic Forest.

Complementary studies to this one should focus on prioritizing the restoration of the Atlantic Forest, such as that developed by Tambosi et al. (2014) in the Atlantic Forest and by Antongiovanni et al. (2022) in the Caatinga, for long-term planning of restoration and regeneration programs, while also accounting for land and social inequality (Melo et al. 2023). Additionally, studies must still focus on how compliance with the FC (restoration of RL and APP in private lands) can be beneficial for the structure of the landscape, such as that carried out by De Marco et al. (2023) in the Cerrado. Finally, there is an urgent need for studies to evaluate the quality of fragments in terms of successional stages, such as that carried out by Dias et al. (2023). Piffer et al. (2022b) point out that fragments regenerated <10 years ago are in the initial stages of regeneration and have limited protection from the AF Law and are mostly deforested, preventing the regeneration process and its benefits for

biodiversity. Thus, Guedes Pinto et al. (2023) propose a review of the Atlantic Forest Law to become a Zero deforestation to prevent loss of forest in initial successional stages. Moreover, expansion of payment programs for ecosystem services (e.g. Conexão Mata Atlântica; https://conexaomataatlantica.mctic.gov.br/cma/portal), can be favorable for forest recovery (Ruggiero et al., 2019).

5 Conclusion

To our knowledge, this is the first study that analyzed the spatiotemporal dynamics of the entire Atlantic Forest landscape structure through multiple landscape metrics, considering a broad tri-national delimitation, not only for forest vegetation but also for other natural vegetation types, and including the effect of linear structure. This study adds to other work carried out in the Caatinga (Antongiovanni et al., 2018), the Cerrado (Pompeu et al., 2024) and the Brazilian Amazon (Guedes Pinto et al., 2023) to understand the dynamics of the landscape structure of these biomes through landscape metrics and propose governance lessons for conservation. Our findings allow a detailed understanding of the habitat fragmentation process in the AF in the last three and a half decades. The number of forest fragments has increased, which comes accompanied by a modest but essential increment of vegetation, mainly from natural regeneration. Besides that, natural vegetation fragments—fundamental to promoting connectivity—are far from being under sufficient protection. Overall, the fragmentation scenarios in Argentina, Brazil, and Paraguay are equally worrying (97% of fragments are very small and highly isolated, and more than half may be under edge effect). We highlight the substantial effect of roads and railways on breaking large FV fragments apart, likely disrupting the functional connectivity of several ecological processes. These findings reinforce the need for conservation and restoration actions considering linear infrastructure, and investing in implementing conservation plans for large fragments. Beyond that, promoting the connectivity of small fragments, managing the matrix to minimize edge effects and improve connectivity, and leading restoration actions in key areas, such as large and isolated fragments, are all measures of great importance. Added to potential coordinated actions, we highlight the importance of planning and building fauna passages to improve landscape connectivity and reduce wildlife roadkill. Finally, the recent increase in vegetation observed in the Atlantic Forest after 2005 appears to be related to two concomitant processes: mostly due to natural regeneration linked to the 2005 protection legislation (AF Law) and a long process of forest transition (abandonment of agricultural land), and to a lesser extent due

to restoration associated with local initiatives such as the Pact for the Restoration of the Atlantic Forest started in 2009 and the implementation of the CAR began in 2012 by the FC. The continuity and expansion of these measures are essential to guarantee the continuity of this vegetation increase process in the future, given the intensified effects of climate change taking place and the further expansion of urban and agricultural areas.

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Data availability

Code for reproducing the analysis is provided in GitHub (https://github.com/LEEClab/ms-atlantic-forest-spatiotemporal-dynamics). Input data and code are provided in Open Science Files (OSF) (https://doi.org/10.17605/OSF.IO/RFWBZ). A comprehensive set of maps presenting the detailed methods and maps for the landscape metrics presented here is found in Vancine et al. (2023).

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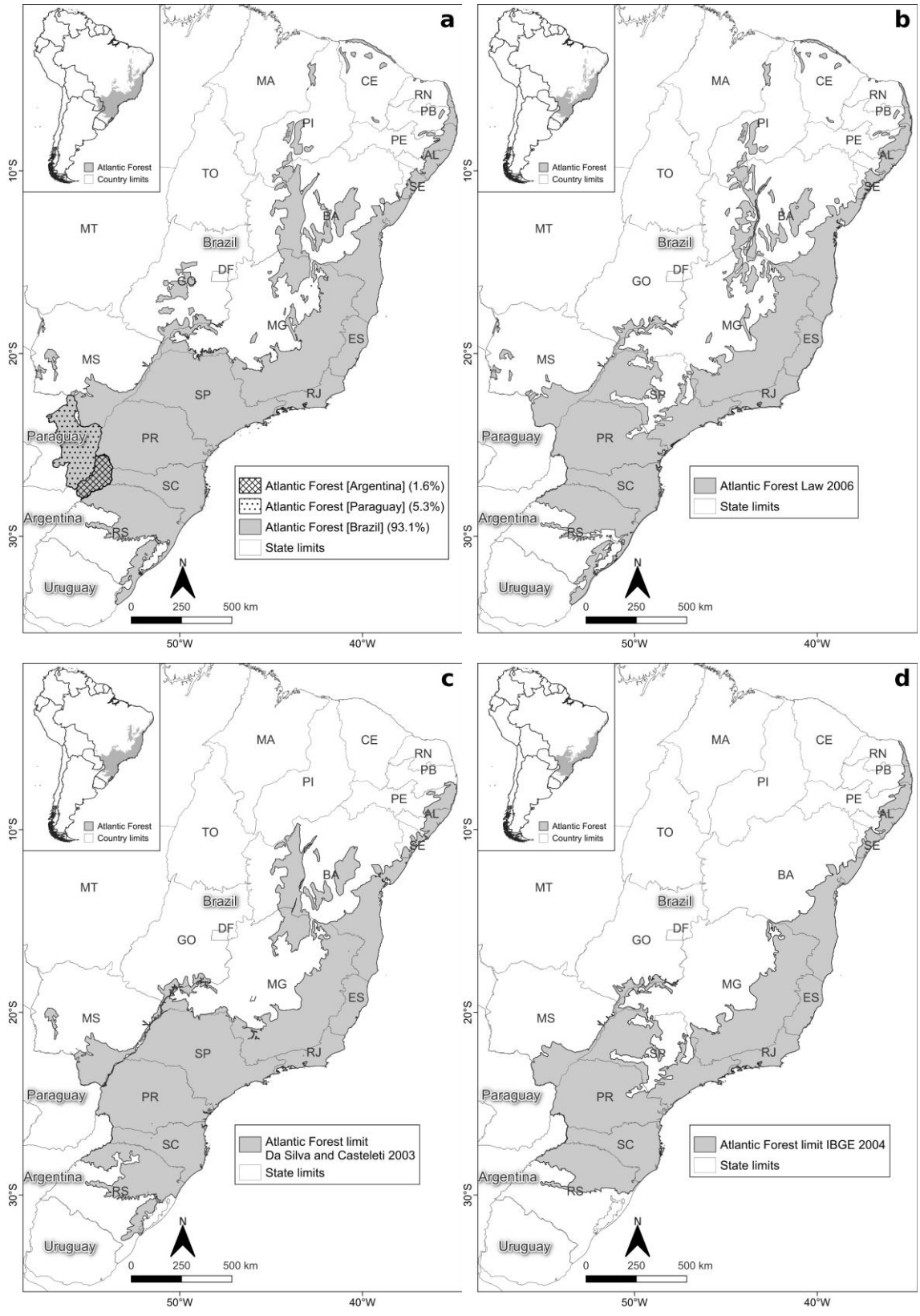
Supplementary material

Data

Roads and railways data were downloaded from official geospatial databases from three countries: Brazil (Instituto Brasileiro de Geografia e Estatística – IBGE; IBGE, 2021), Argentina (Instituto Geográfico Nacional – IGN; IGN, 2022), and Paraguay (Instituto Nacional de Estadística – INE; INE, 2022). The data comprised 14,072 km of railways and 125,483 km of roads, with a total of 139,554 km (Fig. S11). We did not find official railway data for Paraguay, so there may be an underestimation of this effect for this country. For Brazil, we selected paved, operational, and constructed roads, and railways that were selected by relative surface position, and train section for 2021 year. For Argentina, we consider national and provincial roads paved for 2021 year. For Paraguay, we only considered the main roads (according to the Paraguay Atlas nomenclature) for the year 2012, without making a distinction regarding the paving of roads, since this information was not available. We couldn't differentiate the roads and railways by year, as it's almost impossible to find that information, so we used the same layer to trim all the fragments in all years. We assume that this may have overestimated the effect of roads in the past when some of these roads or railways did not exist or were not paved yet. The road and railways layers were rasterized using a parameter that creates densified lines, i.e., all cells touched by the line were included as data for rasterization, which resulted in more densified lines. This guaranteed that the roads and railways would take up space and trimmed the fragments. After rasterizing the lines, the raster covered 528,983 ha (0.33% from the Atlantic Forest delimitation). Thus, we trimmed the fragments of vegetation from the rasterized data.

The Protected Areas (PA) were downloaded from Protected Planet (UNEP-WCMC and IUCN, 2022) for the IUCN categories of protected areas (“Ia”, “Ib”, “II”, “III”, and “IV”) following Rezende et al. (2018), which comprises 986 reserves (4,620,245 ha; 2.84% from AF delimitation) (Fig. S12a). These IUCN categories encompass multiply protection categories for Argentina (Municipal Nature Park, National Park, Nature Monument, Private Refuge, Private Wildlife Refuge, Provincial Park, Strict Nature Reserve, Wilderness Nature Reserve, and Wildlife Reserve), Brazil (Area of Relevant Ecological Interest, Biological Reserve, Ecological Station, Natural Heritage Private Reserve, Natural Monument, Park, Ramsar Site, Wetland of International Importance, Wildlife Refuge), and Paraguay (National Park, Natural Private Reserve, Natural Reserve, Scientific Monument, and Scientific Reserve). The Indigenous Territories (IT) were downloaded for Brazil (Fundação Nacional dos Povos Indígenas; FUNAI, 2020) selecting only “Homologated” and Paraguay (Tierras Indígenas, 2022), which comprises 1023 territories (1,324,973 ha; 0.81% from AF delimitation) (Fig. S12b). We did not find official IT data for Argentina; therefore, we cannot analyze the contribution of IT to this country.

Figures


a
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Atlantic Forest
Country limits
MA
CE
RN
PB
PI
PE
AL
SE
TO
BA
MT
Brazil
DF
GO
MG
ES
MS
SP
RJ
Paraguay
PR
SC
Argentina
RS
Uruguay
10°S
20°S
30°S
50°W
40°W
N
0
250
500 km
Atlantic Forest [Argentina] (1.6%)
Atlantic Forest [Paraguay] (5.3%)
Atlantic Forest [Brazil] (93.1%)
State limits
Atlantic Forest Law 2006
Atlantic Forest limit
Da Silva and Casteleti 2003
Atlantic Forest limit IBGE 2004

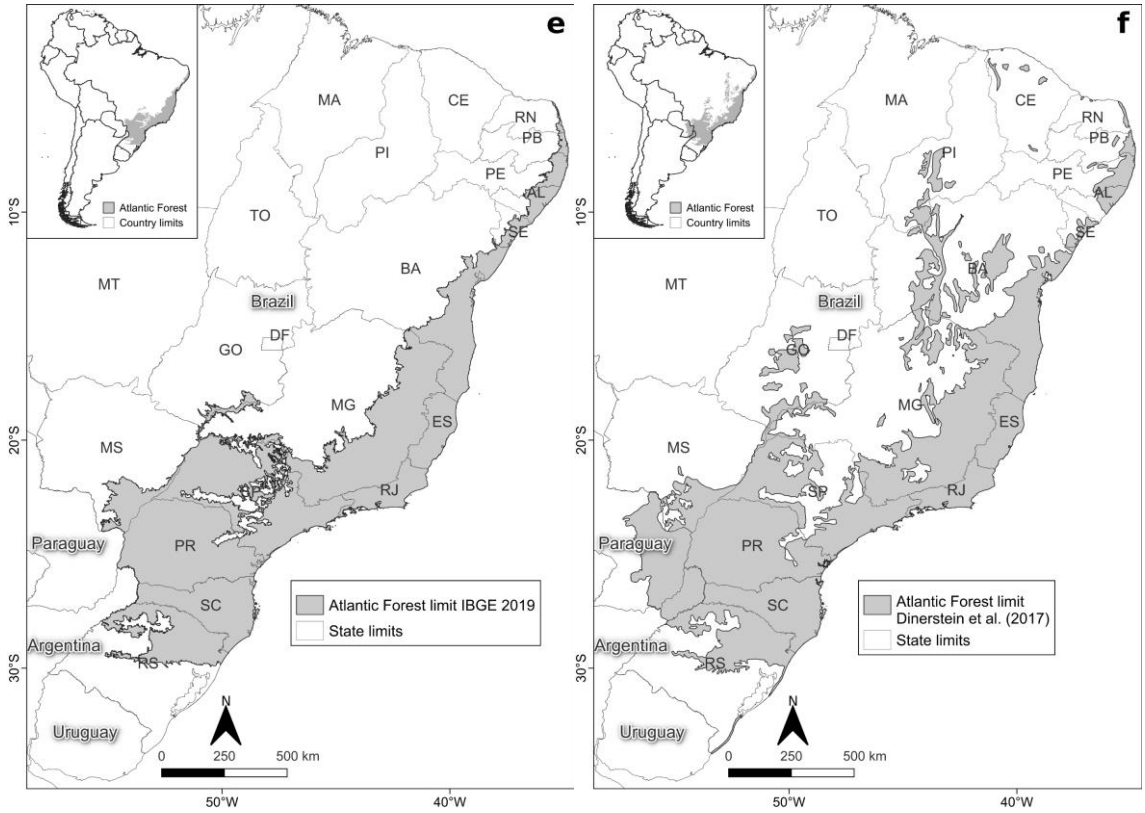
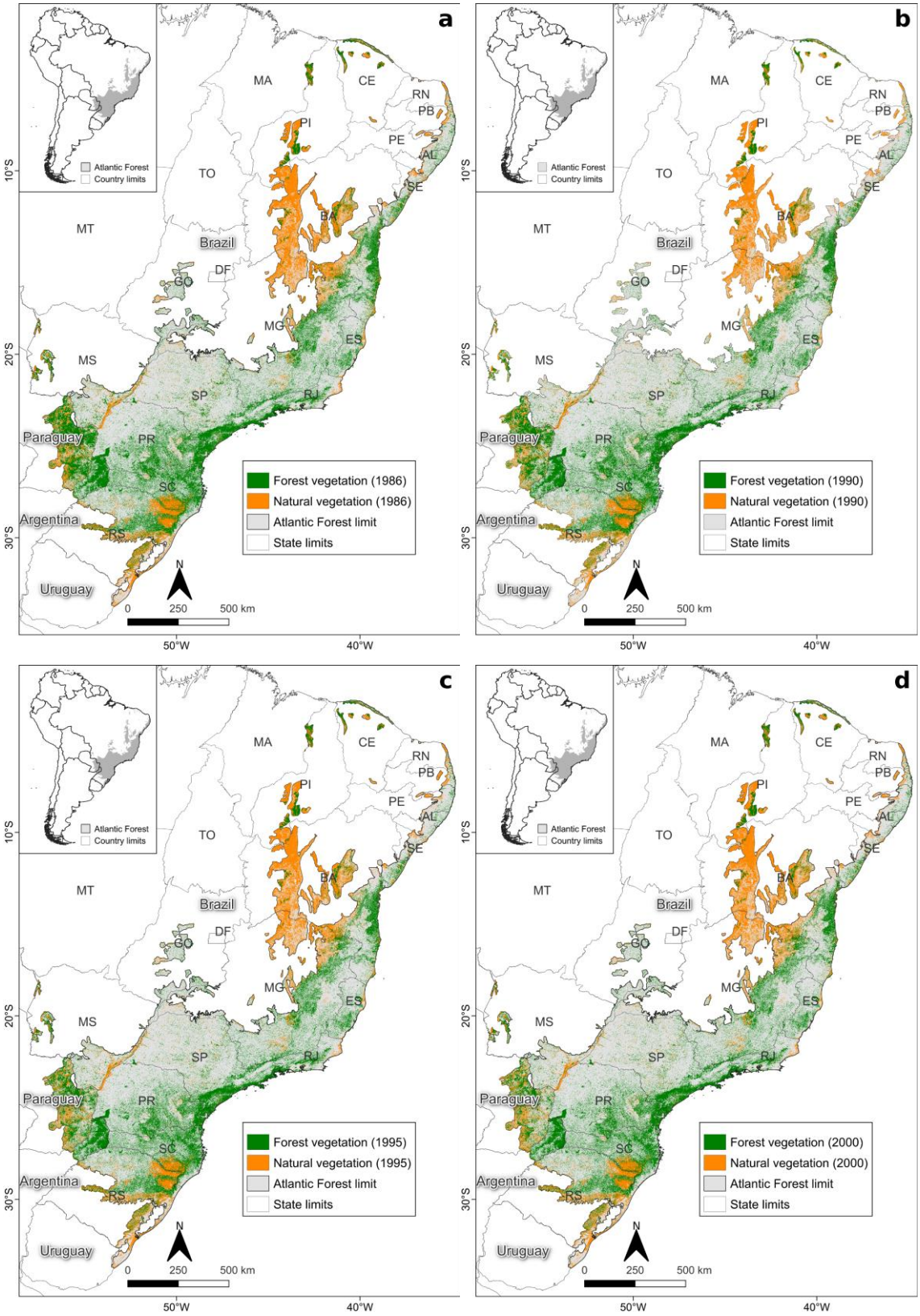


Figure S1. Atlantic Forest delimitation, adapted from Muylaert et al. (2018) (a). Atlantic Forest delimitations used to create the "integrative delimitation" incorporating different types of ecosystems: (b) delimitation defined by Brazilian legislation (Federal Decree No. 750/93 and Atlantic Forest law No. 11 428, of December 22, 2006); (c) delimitation defined by Da Silva and Casteleti (2003); (d) AF delimitation defined by IBGE (2004), (e) AF delimitation defined by IBGE (2019) and; (f) AF delimitation defined by (Dinerstein et al., 2017) and used in the Ecoregions 2017®.


a
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Atlantic Forest
Country limits
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Brazil
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GO
MG
ES
MS
SP
RJ
Paraguay
PR
SC
Argentina
RS
Uruguay
Forest vegetation (1986)
Natural vegetation (1986)
Atlantic Forest limit
State limits
Forest vegetation (1990)
Natural vegetation (1990)
Atlantic Forest limit
State limits
Forest vegetation (1995)
Natural vegetation (1995)
Atlantic Forest limit
State limits
Forest vegetation (2000)
Natural vegetation (2000)
Atlantic Forest limit
State limits
N
0
250
500 km
10°S
20°S
30°S
50°W
40°W

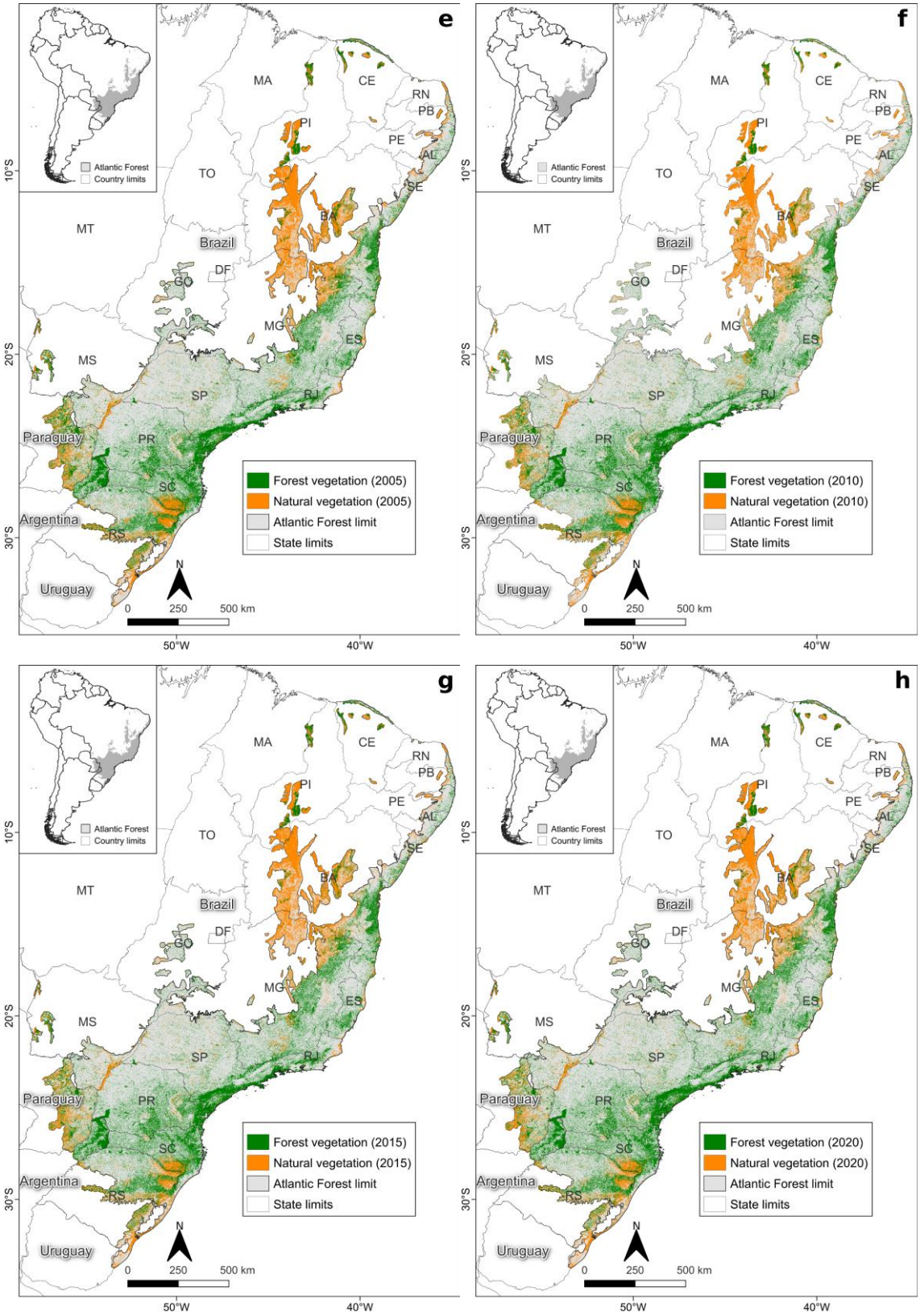
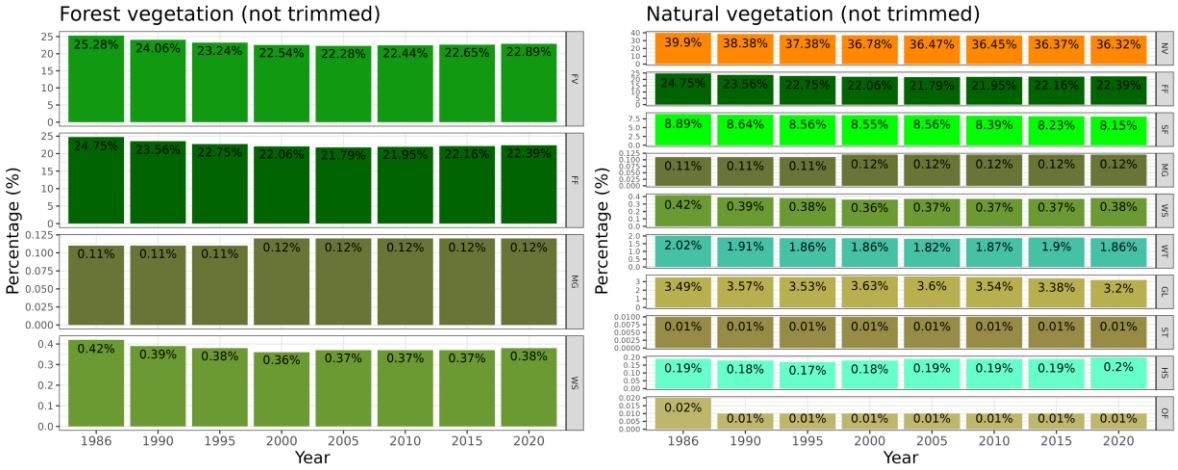
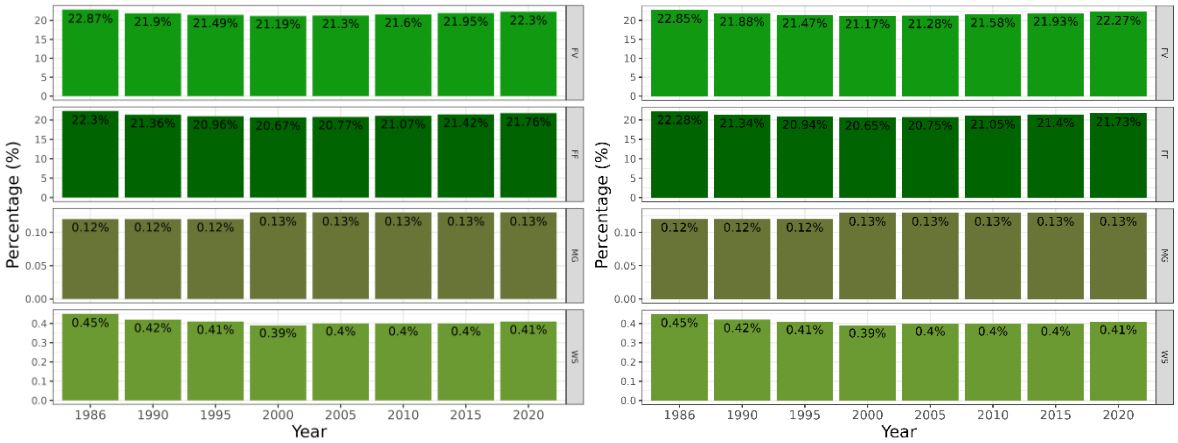


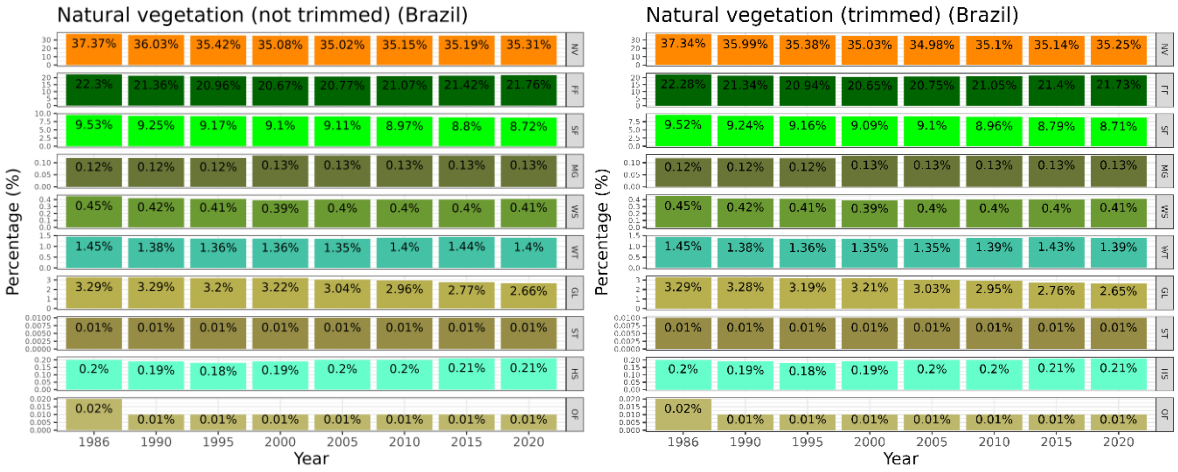
Figure S2. Forest Vegetation (FV) and Natural Vegetation (NV) cover for the entire Atlantic Forest from 1986-2020 (a-h). Note that the group of vegetation classes NV comprises both forests (FV, in green) and other non-forest natural vegetation classes (in orange).


Forest vegetation (not trimmed)
Percentage (%)
Year
FV
FF
MG
WS
25.28% 24.06% 23.24% 22.54% 22.28% 22.44% 22.65% 22.89%
24.75% 23.56% 22.75% 22.06% 21.79% 21.95% 22.16% 22.39%
0.11% 0.11% 0.11% 0.12% 0.12% 0.12% 0.12% 0.12%
0.42% 0.39% 0.38% 0.36% 0.37% 0.37% 0.37% 0.38%
1986 1990 1995 2000 2005 2010 2015 2020

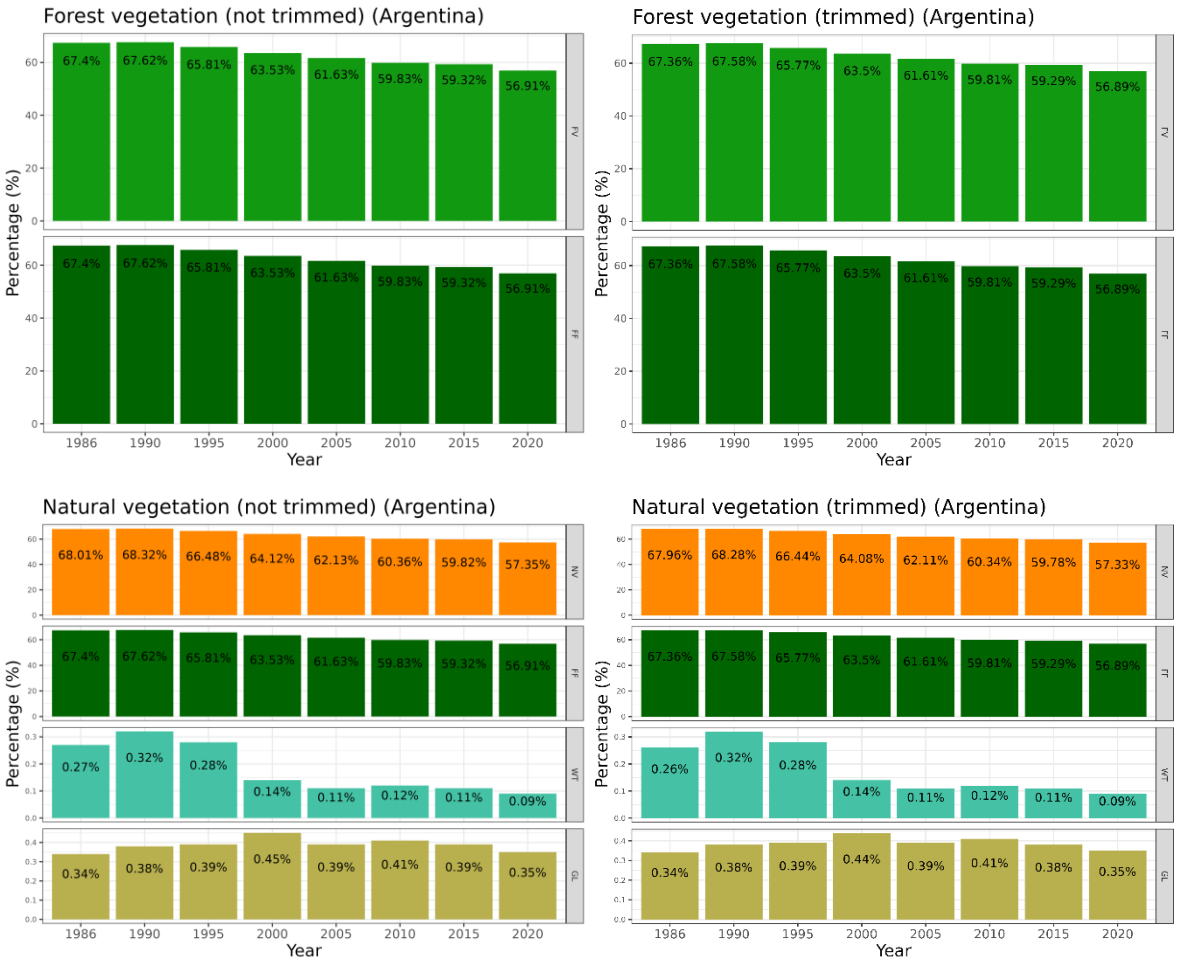
Natural vegetation (not trimmed)
Percentage (%)
Year
NV
FF
SF
MG
WS
WT
GL
ST
HS
OF
39.9% 38.38% 37.38% 36.78% 36.47% 36.45% 36.37% 36.32%
24.75% 23.56% 22.75% 22.06% 21.79% 21.95% 22.16% 22.39%
8.89% 8.64% 8.56% 8.55% 8.56% 8.39% 8.23% 8.15%
0.11% 0.11% 0.11% 0.12% 0.12% 0.12% 0.12% 0.12%
0.42% 0.39% 0.38% 0.36% 0.37% 0.37% 0.37% 0.38%
2.02% 1.91% 1.86% 1.86% 1.82% 1.87% 1.9% 1.86%
3.49% 3.57% 3.53% 3.63% 3.6% 3.54% 3.38% 3.2%
0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01%
0.19% 0.18% 0.17% 0.18% 0.19% 0.19% 0.19% 0.2%
0.02% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01%
1986 1990 1995 2000 2005 2010 2015 2020


Forest vegetation (not trimmed) (Brazil)
Percentage (%)
Year
FV
FF
MG
WS
22.87% 21.9% 21.49% 21.19% 21.3% 21.6% 21.95% 22.3%
22.3% 21.36% 20.96% 20.67% 20.77% 21.07% 21.42% 21.76%
0.12% 0.12% 0.12% 0.13% 0.13% 0.13% 0.13% 0.13%
0.45% 0.42% 0.41% 0.39% 0.4% 0.4% 0.4% 0.41%
1986 1990 1995 2000 2005 2010 2015 2020

Forest vegetation (trimmed) (Brazil)
Percentage (%)
Year
FV
FF
MG
WS
22.85% 21.88% 21.47% 21.17% 21.28% 21.58% 21.93% 22.27%
22.28% 21.34% 20.94% 20.65% 20.75% 21.05% 21.4% 21.73%
0.12% 0.12% 0.12% 0.13% 0.13% 0.13% 0.13% 0.13%
0.45% 0.42% 0.41% 0.39% 0.4% 0.4% 0.4% 0.41%
1986 1990 1995 2000 2005 2010 2015 2020


Natural vegetation (not trimmed) (Brazil)
Percentage (%)
Year
NV
FF
SF
MG
WS
WT
GL
ST
HS
OF
37.37% 36.03% 35.42% 35.08% 35.02% 35.15% 35.19% 35.31%
22.3% 21.36% 20.96% 20.67% 20.77% 21.07% 21.42% 21.76%
9.53% 9.25% 9.17% 9.1% 9.11% 8.97% 8.8% 8.72%
0.12% 0.12% 0.12% 0.13% 0.13% 0.13% 0.13% 0.13%
0.45% 0.42% 0.41% 0.39% 0.4% 0.4% 0.4% 0.41%
1.45% 1.38% 1.36% 1.36% 1.35% 1.4% 1.44% 1.4%
3.29% 3.29% 3.2% 3.22% 3.04% 2.96% 2.77% 2.66%
0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01%
0.2% 0.19% 0.18% 0.19% 0.2% 0.2% 0.21% 0.21%
0.02% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01%
1986 1990 1995 2000 2005 2010 2015 2020

Natural vegetation (trimmed) (Brazil)
Percentage (%)
Year
NV
FF
SF
MG
WS
WT
GL
ST
HS
OF
37.34% 35.99% 35.38% 35.03% 34.98% 35.1% 35.14% 35.25%
22.28% 21.34% 20.94% 20.65% 20.75% 21.05% 21.4% 21.73%
9.52% 9.24% 9.16% 9.09% 9.1% 8.96% 8.79% 8.71%
0.12% 0.12% 0.12% 0.13% 0.13% 0.13% 0.13% 0.13%
0.45% 0.42% 0.41% 0.39% 0.4% 0.4% 0.4% 0.41%
1.45% 1.38% 1.36% 1.35% 1.35% 1.39% 1.43% 1.39%
3.29% 3.28% 3.19% 3.21% 3.03% 2.95% 2.76% 2.65%
0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01%
0.2% 0.19% 0.18% 0.19% 0.2% 0.2% 0.21% 0.21%
0.02% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01% 0.01%
1986 1990 1995 2000 2005 2010 2015 2020


Forest vegetation (not trimmed) (Argentina)
Percentage (%)
67.4% 67.62% 65.81% 63.53% 61.63% 59.83% 59.32% 56.91%
67.4% 67.62% 65.81% 63.53% 61.63% 59.83% 59.32% 56.91%
1986 1990 1995 2000 2005 2010 2015 2020
Year
Forest vegetation (trimmed) (Argentina)
Percentage (%)
67.36% 67.58% 65.77% 63.5% 61.61% 59.81% 59.29% 56.89%
67.36% 67.58% 65.77% 63.5% 61.61% 59.81% 59.29% 56.89%
1986 1990 1995 2000 2005 2010 2015 2020
Year
Natural vegetation (not trimmed) (Argentina)
Percentage (%)
68.01% 68.32% 66.48% 64.12% 62.13% 60.36% 59.82% 57.35%
67.4% 67.62% 65.81% 63.53% 61.63% 59.83% 59.32% 56.91%
0.27% 0.32% 0.28% 0.14% 0.11% 0.12% 0.11% 0.09%
0.34% 0.38% 0.39% 0.45% 0.39% 0.41% 0.39% 0.35%
1986 1990 1995 2000 2005 2010 2015 2020
Year
Natural vegetation (trimmed) (Argentina)
Percentage (%)
67.96% 68.28% 66.44% 64.08% 62.11% 60.34% 59.78% 57.33%
67.36% 67.58% 65.77% 63.5% 61.61% 59.81% 59.29% 56.89%
0.26% 0.32% 0.28% 0.14% 0.11% 0.12% 0.11% 0.09%
0.34% 0.38% 0.39% 0.44% 0.39% 0.41% 0.38% 0.35%
1986 1990 1995 2000 2005 2010 2015 2020
Year

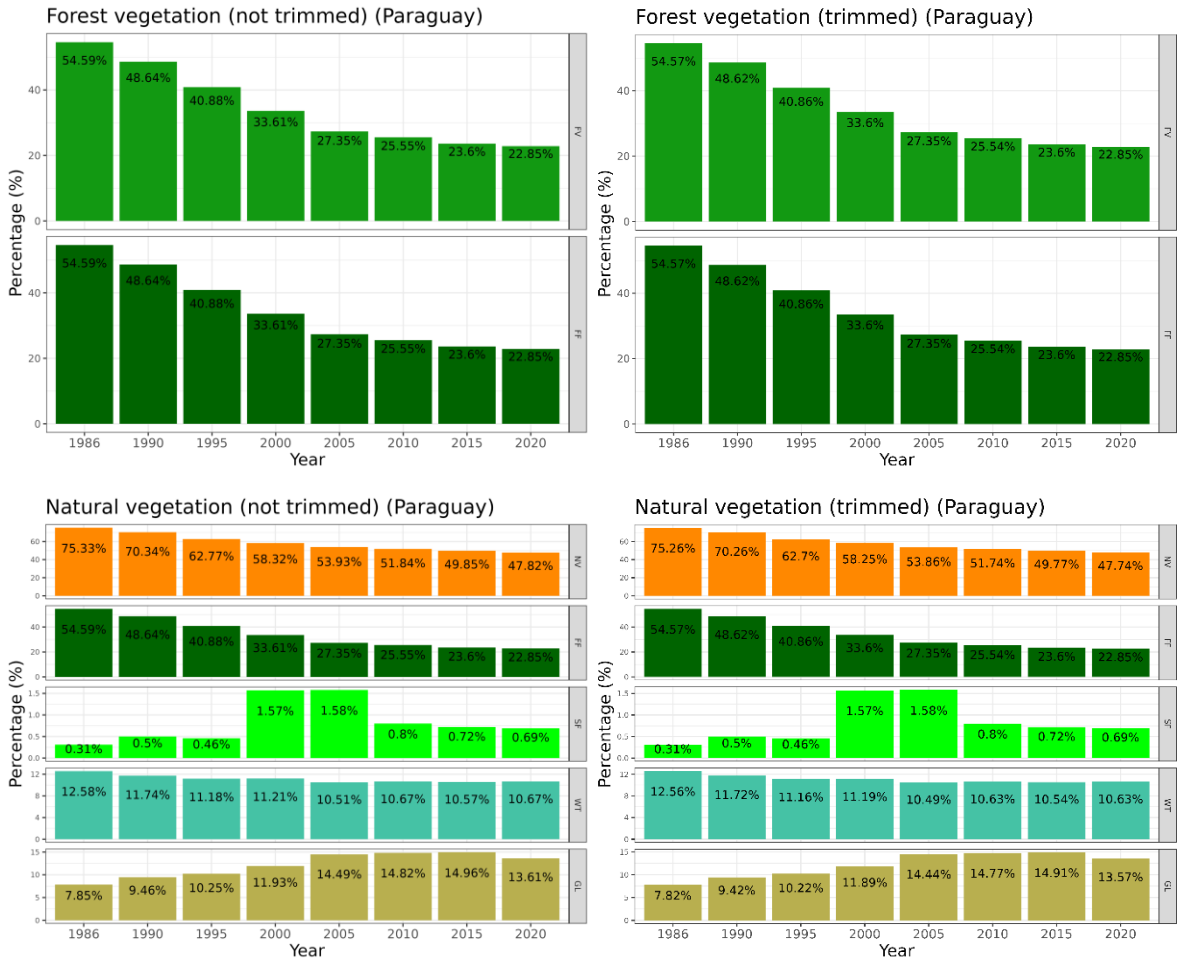
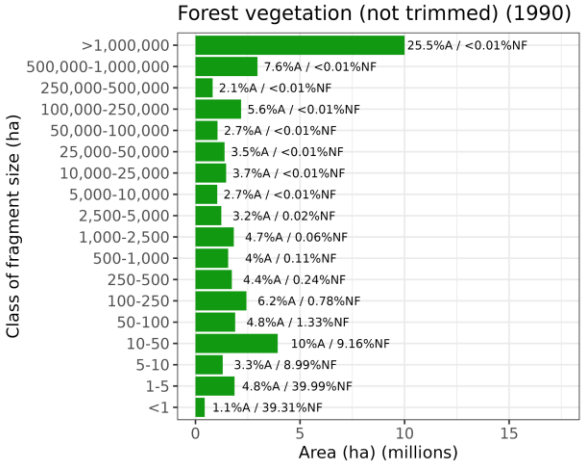
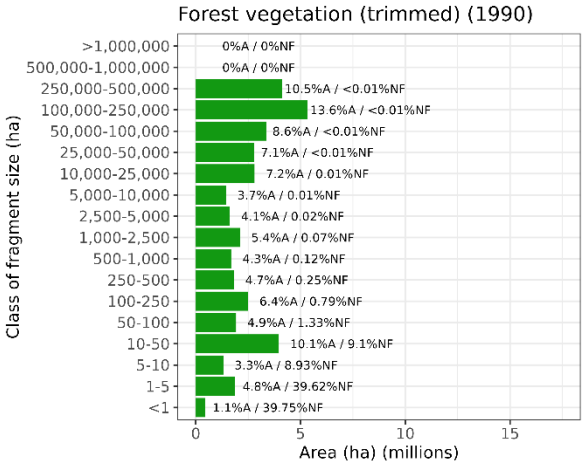
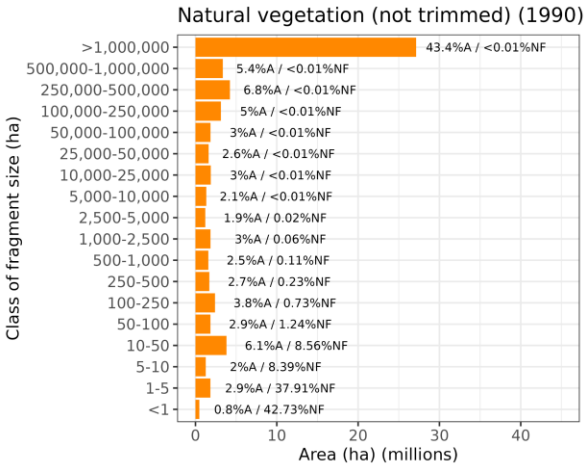
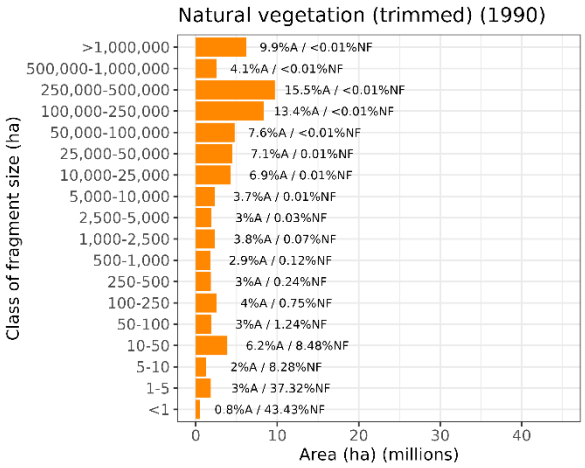


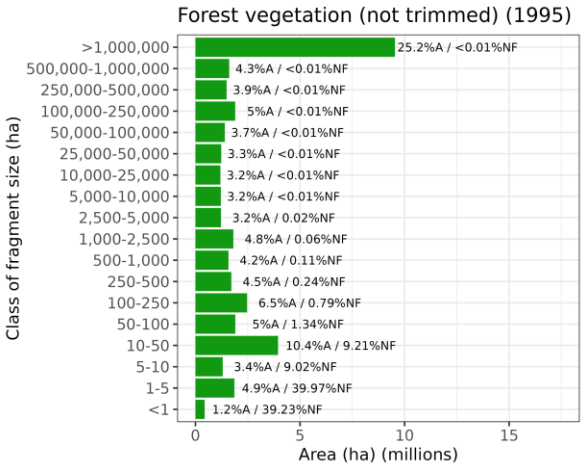
Figure S3. Forest Vegetation (FV) and Natural Vegetation (NV) cover per year for the entire Atlantic Forest, Brazil, Argentina, and Paraguay, trimmed and not trimmed by roads and railways. Abbreviations for FV cover are: FV = Forest vegetation, FF = Forest formation, MG = Mangrove, WS = Wooded sandbank vegetation (*restinga*). Abbreviations for NV cover are: NV = Natural vegetation, FF = Forest formation, SF = Savanna formation, MG = Mangrove, WS = Wooded sandbank vegetation (*restinga*), WT = Wetland, GL = Grassland, ST = Salt flat, HS = Herbaceous sandbank vegetation, OF = Other non-forest formations. Class colors follow MapBiomas collection 7 and MapBiomas Bosque Atlántico collection 2 legends.

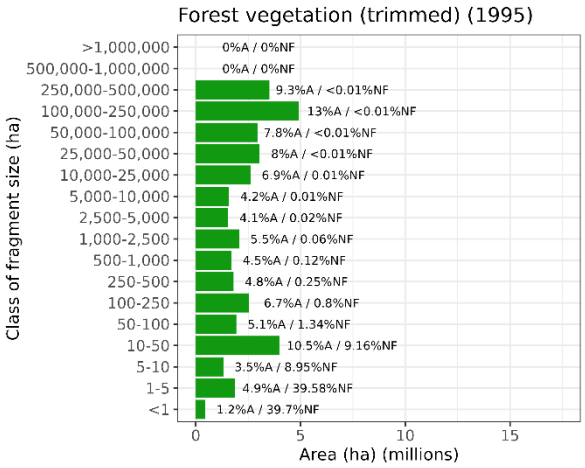

Forest vegetation (not trimmed) (1990)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
25.5%A / <0.01%NF
7.6%A / <0.01%NF
2.1%A / <0.01%NF
5.6%A / <0.01%NF
2.7%A / <0.01%NF
3.5%A / <0.01%NF
3.7%A / <0.01%NF
2.7%A / <0.01%NF
3.2%A / 0.02%NF
4.7%A / 0.06%NF
4%A / 0.11%NF
4.4%A / 0.24%NF
6.2%A / 0.78%NF
4.8%A / 1.33%NF
10%A / 9.16%NF
3.3%A / 8.99%NF
4.8%A / 39.99%NF
1.1%A / 39.31%NF
0
5
10
15
Area (ha) (millions)

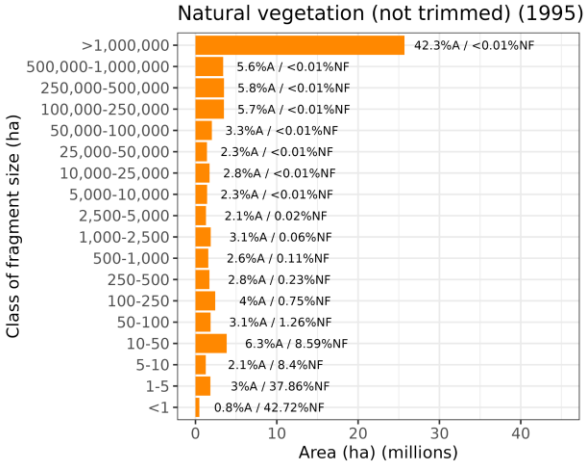

Forest vegetation (trimmed) (1990)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
0%A / 0%NF
0%A / 0%NF
10.5%A / <0.01%NF
13.6%A / <0.01%NF
8.6%A / <0.01%NF
7.1%A / <0.01%NF
7.2%A / 0.01%NF
3.7%A / 0.01%NF
4.1%A / 0.02%NF
5.4%A / 0.07%NF
4.3%A / 0.12%NF
4.7%A / 0.25%NF
6.4%A / 0.79%NF
4.9%A / 1.33%NF
10.1%A / 9.1%NF
3.3%A / 8.93%NF
4.8%A / 39.62%NF
1.1%A / 39.75%NF
0
5
10
15
Area (ha) (millions)

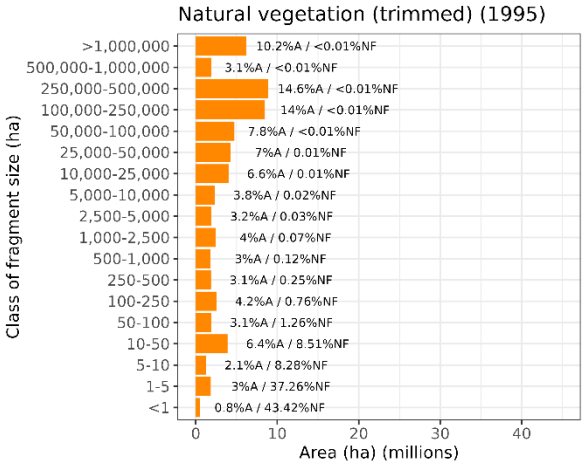

Natural vegetation (not trimmed) (1990)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
43.4%A / <0.01%NF
5.4%A / <0.01%NF
6.8%A / <0.01%NF
5%A / <0.01%NF
3%A / <0.01%NF
2.6%A / <0.01%NF
3%A / <0.01%NF
2.1%A / <0.01%NF
1.9%A / 0.02%NF
3%A / 0.06%NF
2.5%A / 0.11%NF
2.7%A / 0.23%NF
3.8%A / 0.73%NF
2.9%A / 1.24%NF
6.1%A / 8.56%NF
2%A / 8.39%NF
2.9%A / 37.91%NF
0.8%A / 42.73%NF
0
10
20
30
40
Area (ha) (millions)

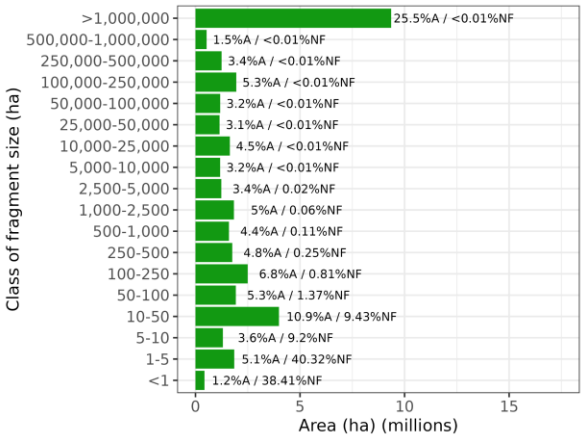

Natural vegetation (trimmed) (1990)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
9.9%A / <0.01%NF
4.1%A / <0.01%NF
15.5%A / <0.01%NF
13.4%A / <0.01%NF
7.6%A / <0.01%NF
7.1%A / 0.01%NF
6.9%A / 0.01%NF
3.7%A / 0.01%NF
3%A / 0.03%NF
3.8%A / 0.07%NF
2.9%A / 0.12%NF
3%A / 0.24%NF
4%A / 0.75%NF
3%A / 1.24%NF
6.2%A / 8.48%NF
2%A / 8.28%NF
3%A / 37.32%NF
0.8%A / 43.43%NF
0
10
20
30
40
Area (ha) (millions)

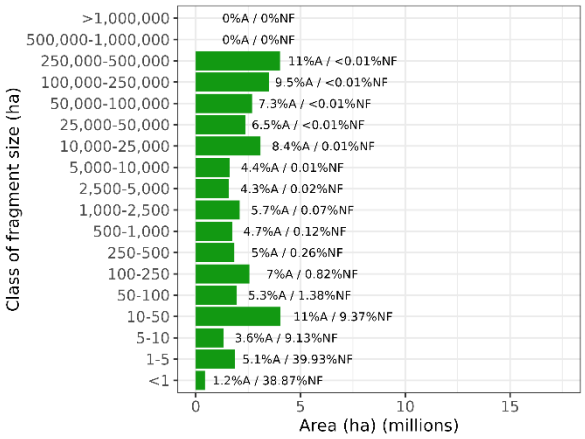

Forest vegetation (not trimmed) (1995)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
25.2%A / <0.01%NF
4.3%A / <0.01%NF
3.9%A / <0.01%NF
5%A / <0.01%NF
3.7%A / <0.01%NF
3.3%A / <0.01%NF
3.2%A / <0.01%NF
3.2%A / <0.01%NF
3.2%A / 0.02%NF
4.8%A / 0.06%NF
4.2%A / 0.11%NF
4.5%A / 0.24%NF
6.5%A / 0.79%NF
5%A / 1.34%NF
10.4%A / 9.21%NF
3.4%A / 9.02%NF
4.9%A / 39.97%NF
1.2%A / 39.23%NF
0
5
10
15
Area (ha) (millions)

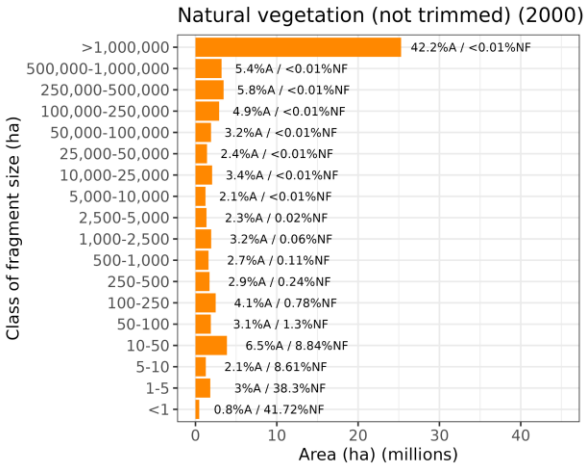

Forest vegetation (trimmed) (1995)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
0%A / 0%NF
0%A / 0%NF
9.3%A / <0.01%NF
13%A / <0.01%NF
7.8%A / <0.01%NF
8%A / <0.01%NF
6.9%A / 0.01%NF
4.2%A / 0.01%NF
4.1%A / 0.02%NF
5.5%A / 0.06%NF
4.5%A / 0.12%NF
4.8%A / 0.25%NF
6.7%A / 0.8%NF
5.1%A / 1.34%NF
10.5%A / 9.16%NF
3.5%A / 8.95%NF
4.9%A / 39.58%NF
1.2%A / 39.7%NF
0
5
10
15
Area (ha) (millions)

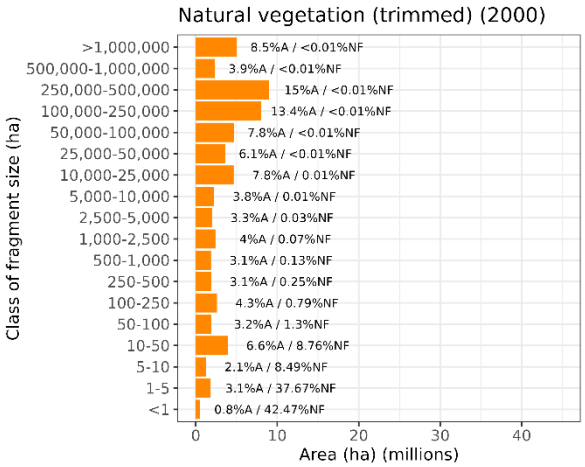

Natural vegetation (not trimmed) (1995)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
42.3%A / <0.01%NF
5.6%A / <0.01%NF
5.8%A / <0.01%NF
5.7%A / <0.01%NF
3.3%A / <0.01%NF
2.3%A / <0.01%NF
2.8%A / <0.01%NF
2.3%A / <0.01%NF
2.1%A / 0.02%NF
3.1%A / 0.06%NF
2.6%A / 0.11%NF
2.8%A / 0.23%NF
4%A / 0.75%NF
3.1%A / 1.26%NF
6.3%A / 8.59%NF
2.1%A / 8.4%NF
3%A / 37.86%NF
0.8%A / 42.72%NF
0
10
20
30
40
Area (ha) (millions)

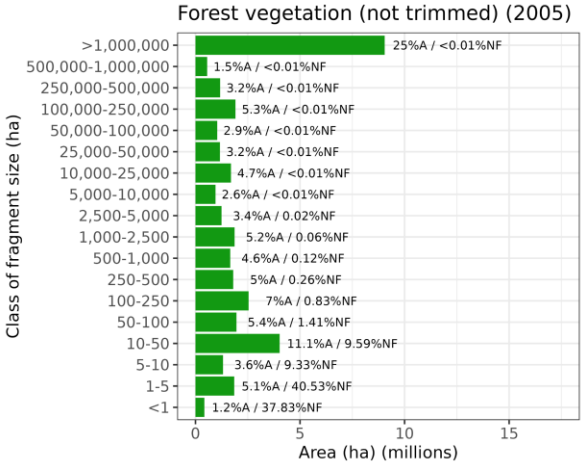

Natural vegetation (trimmed) (1995)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
10.2%A / <0.01%NF
3.1%A / <0.01%NF
14.6%A / <0.01%NF
14%A / <0.01%NF
7.8%A / <0.01%NF
7%A / 0.01%NF
6.6%A / 0.01%NF
3.8%A / 0.02%NF
3.2%A / 0.03%NF
4%A / 0.07%NF
3%A / 0.12%NF
3.1%A / 0.25%NF
4.2%A / 0.76%NF
3.1%A / 1.26%NF
6.4%A / 8.51%NF
2.1%A / 8.28%NF
3%A / 37.26%NF
0.8%A / 43.42%NF
0
10
20
30
40
Area (ha) (millions)

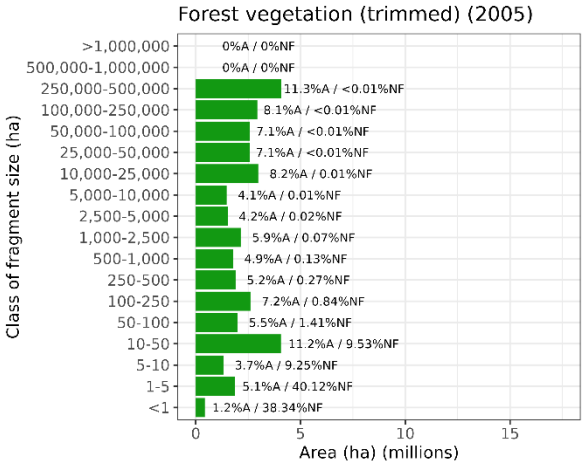

Forest vegetation (not trimmed) (2000)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
25.5%A / <0.01%NF
1.5%A / <0.01%NF
3.4%A / <0.01%NF
5.3%A / <0.01%NF
3.2%A / <0.01%NF
3.1%A / <0.01%NF
4.5%A / <0.01%NF
3.2%A / <0.01%NF
3.4%A / 0.02%NF
5%A / 0.06%NF
4.4%A / 0.11%NF
4.8%A / 0.25%NF
6.8%A / 0.81%NF
5.3%A / 1.37%NF
10.9%A / 9.43%NF
3.6%A / 9.2%NF
5.1%A / 40.32%NF
1.2%A / 38.41%NF
0
5
10
15
Area (ha) (millions)

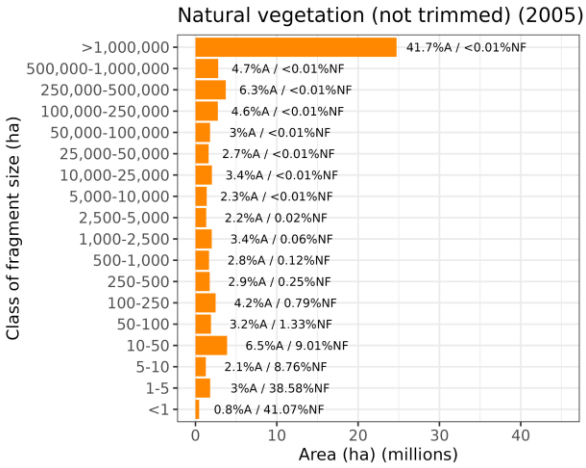

Forest vegetation (trimmed) (2000)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
0%A / 0%NF
0%A / 0%NF
11%A / <0.01%NF
9.5%A / <0.01%NF
7.3%A / <0.01%NF
6.5%A / <0.01%NF
8.4%A / 0.01%NF
4.4%A / 0.01%NF
4.3%A / 0.02%NF
5.7%A / 0.07%NF
4.7%A / 0.12%NF
5%A / 0.26%NF
7%A / 0.82%NF
5.3%A / 1.38%NF
11%A / 9.37%NF
3.6%A / 9.13%NF
5.1%A / 39.93%NF
1.2%A / 38.87%NF
0
5
10
15
Area (ha) (millions)

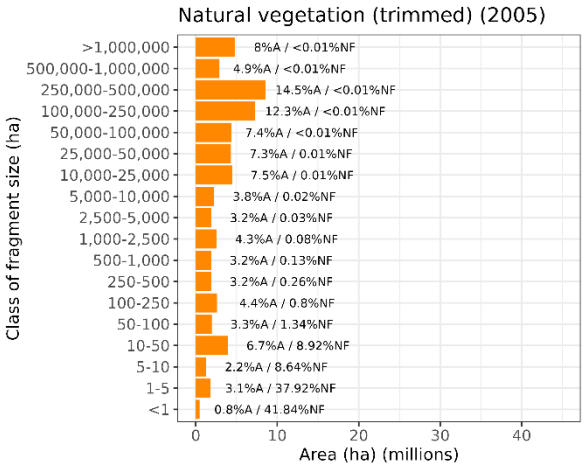

Natural vegetation (not trimmed) (2000)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
42.2%A / <0.01%NF
5.4%A / <0.01%NF
5.8%A / <0.01%NF
4.9%A / <0.01%NF
3.2%A / <0.01%NF
2.4%A / <0.01%NF
3.4%A / <0.01%NF
2.1%A / <0.01%NF
2.3%A / 0.02%NF
3.2%A / 0.06%NF
2.7%A / 0.11%NF
2.9%A / 0.24%NF
4.1%A / 0.78%NF
3.1%A / 1.3%NF
6.5%A / 8.84%NF
2.1%A / 8.61%NF
3%A / 38.3%NF
0.8%A / 41.72%NF
0
10
20
30
40
Area (ha) (millions)

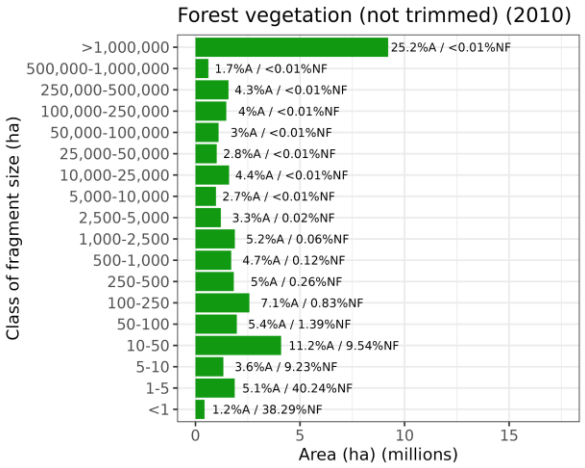

Natural vegetation (trimmed) (2000)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
8.5%A / <0.01%NF
3.9%A / <0.01%NF
15%A / <0.01%NF
13.4%A / <0.01%NF
7.8%A / <0.01%NF
6.1%A / <0.01%NF
7.8%A / 0.01%NF
3.8%A / 0.01%NF
3.3%A / 0.03%NF
4%A / 0.07%NF
3.1%A / 0.13%NF
3.1%A / 0.25%NF
4.3%A / 0.79%NF
3.2%A / 1.3%NF
6.6%A / 8.76%NF
2.1%A / 8.49%NF
3.1%A / 37.67%NF
0.8%A / 42.47%NF
0
10
20
30
40
Area (ha) (millions)

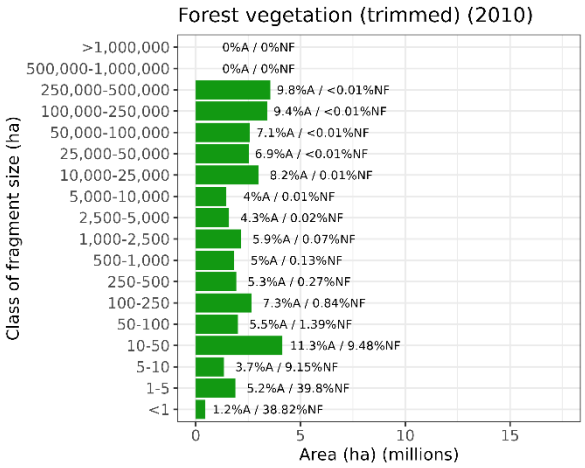

Forest vegetation (not trimmed) (2005)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
25%A / <0.01%NF
1.5%A / <0.01%NF
3.2%A / <0.01%NF
5.3%A / <0.01%NF
2.9%A / <0.01%NF
3.2%A / <0.01%NF
4.7%A / <0.01%NF
2.6%A / <0.01%NF
3.4%A / 0.02%NF
5.2%A / 0.06%NF
4.6%A / 0.12%NF
5%A / 0.26%NF
7%A / 0.83%NF
5.4%A / 1.41%NF
11.1%A / 9.59%NF
3.6%A / 9.33%NF
5.1%A / 40.53%NF
1.2%A / 37.83%NF
0
5
10
15
Area (ha) (millions)


Forest vegetation (trimmed) (2005)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
0%A / 0%NF
0%A / 0%NF
11.3%A / <0.01%NF
8.1%A / <0.01%NF
7.1%A / <0.01%NF
7.1%A / <0.01%NF
8.2%A / 0.01%NF
4.1%A / 0.01%NF
4.2%A / 0.02%NF
5.9%A / 0.07%NF
4.9%A / 0.13%NF
5.2%A / 0.27%NF
7.2%A / 0.84%NF
5.5%A / 1.41%NF
11.2%A / 9.53%NF
3.7%A / 9.25%NF
5.1%A / 40.12%NF
1.2%A / 38.34%NF
0
5
10
15
Area (ha) (millions)


Natural vegetation (not trimmed) (2005)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
41.7%A / <0.01%NF
4.7%A / <0.01%NF
6.3%A / <0.01%NF
4.6%A / <0.01%NF
3%A / <0.01%NF
2.7%A / <0.01%NF
3.4%A / <0.01%NF
2.3%A / <0.01%NF
2.2%A / 0.02%NF
3.4%A / 0.06%NF
2.8%A / 0.12%NF
2.9%A / 0.25%NF
4.2%A / 0.79%NF
3.2%A / 1.33%NF
6.5%A / 9.01%NF
2.1%A / 8.76%NF
3%A / 38.58%NF
0.8%A / 41.07%NF
0
10
20
30
40
Area (ha) (millions)


Natural vegetation (trimmed) (2005)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
8%A / <0.01%NF
4.9%A / <0.01%NF
14.5%A / <0.01%NF
12.3%A / <0.01%NF
7.4%A / <0.01%NF
7.3%A / 0.01%NF
7.5%A / 0.01%NF
3.8%A / 0.02%NF
3.2%A / 0.03%NF
4.3%A / 0.08%NF
3.2%A / 0.13%NF
3.2%A / 0.26%NF
4.4%A / 0.8%NF
3.3%A / 1.34%NF
6.7%A / 8.92%NF
2.2%A / 8.64%NF
3.1%A / 37.92%NF
0.8%A / 41.84%NF
0
10
20
30
40
Area (ha) (millions)


Forest vegetation (not trimmed) (2010)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
25.2%A / <0.01%NF
1.7%A / <0.01%NF
4.3%A / <0.01%NF
4%A / <0.01%NF
3%A / <0.01%NF
2.8%A / <0.01%NF
4.4%A / <0.01%NF
2.7%A / <0.01%NF
3.3%A / 0.02%NF
5.2%A / 0.06%NF
4.7%A / 0.12%NF
5%A / 0.26%NF
7.1%A / 0.83%NF
5.4%A / 1.39%NF
11.2%A / 9.54%NF
3.6%A / 9.23%NF
5.1%A / 40.24%NF
1.2%A / 38.29%NF
0
5
10
15
Area (ha) (millions)


Forest vegetation (trimmed) (2010)
Class of fragment size (ha)
>1,000,000
500,000-1,000,000
250,000-500,000
100,000-250,000
50,000-100,000
25,000-50,000
10,000-25,000
5,000-10,000
2,500-5,000
1,000-2,500
500-1,000
250-500
100-250
50-100
10-50
5-10
1-5
<1
0%A / 0%NF
0%A / 0%NF
9.8%A / <0.01%NF
9.4%A / <0.01%NF
7.1%A / <0.01%NF
6.9%A / <0.01%NF
8.2%A / 0.01%NF
4%A / 0.01%NF
4.3%A / 0.02%NF
5.9%A / 0.07%NF
5%A / 0.13%NF
5.3%A / 0.27%NF
7.3%A / 0.84%NF
5.5%A / 1.39%NF
11.3%A / 9.48%NF
3.7%A / 9.15%NF
5.2%A / 39.8%NF
1.2%A / 38.82%NF
0
5
10
15
Area (ha) (millions)

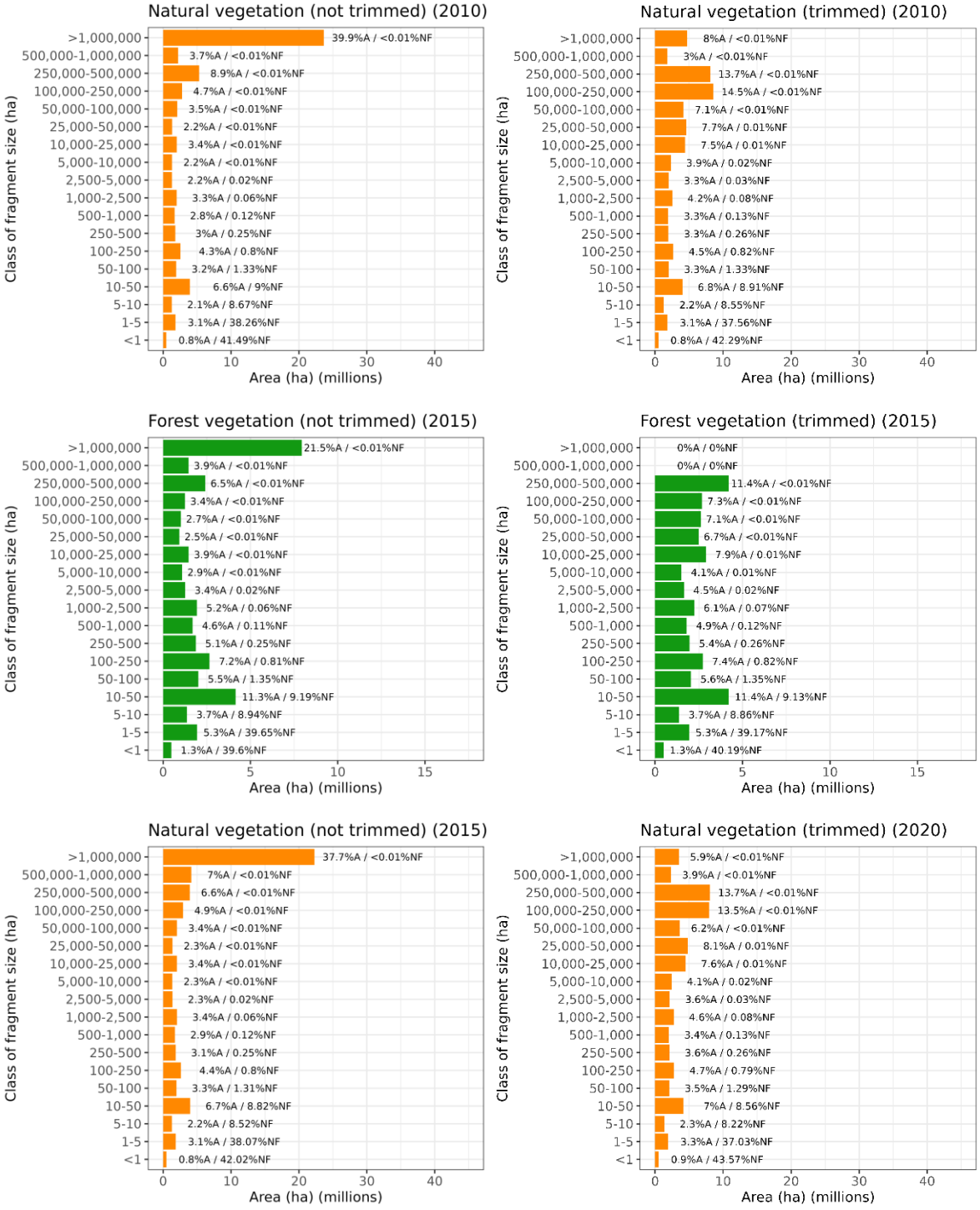


Figure S4. Size distribution of Forest Vegetation (FV) and Natural Vegetation (NV) fragments in the Atlantic Forest (1990-2015), without and with road and railways effect. %A: percentage of total area; %NP: percentage of number of fragments. For the years 1986 and 2020, see Fig. 2 in the main text.

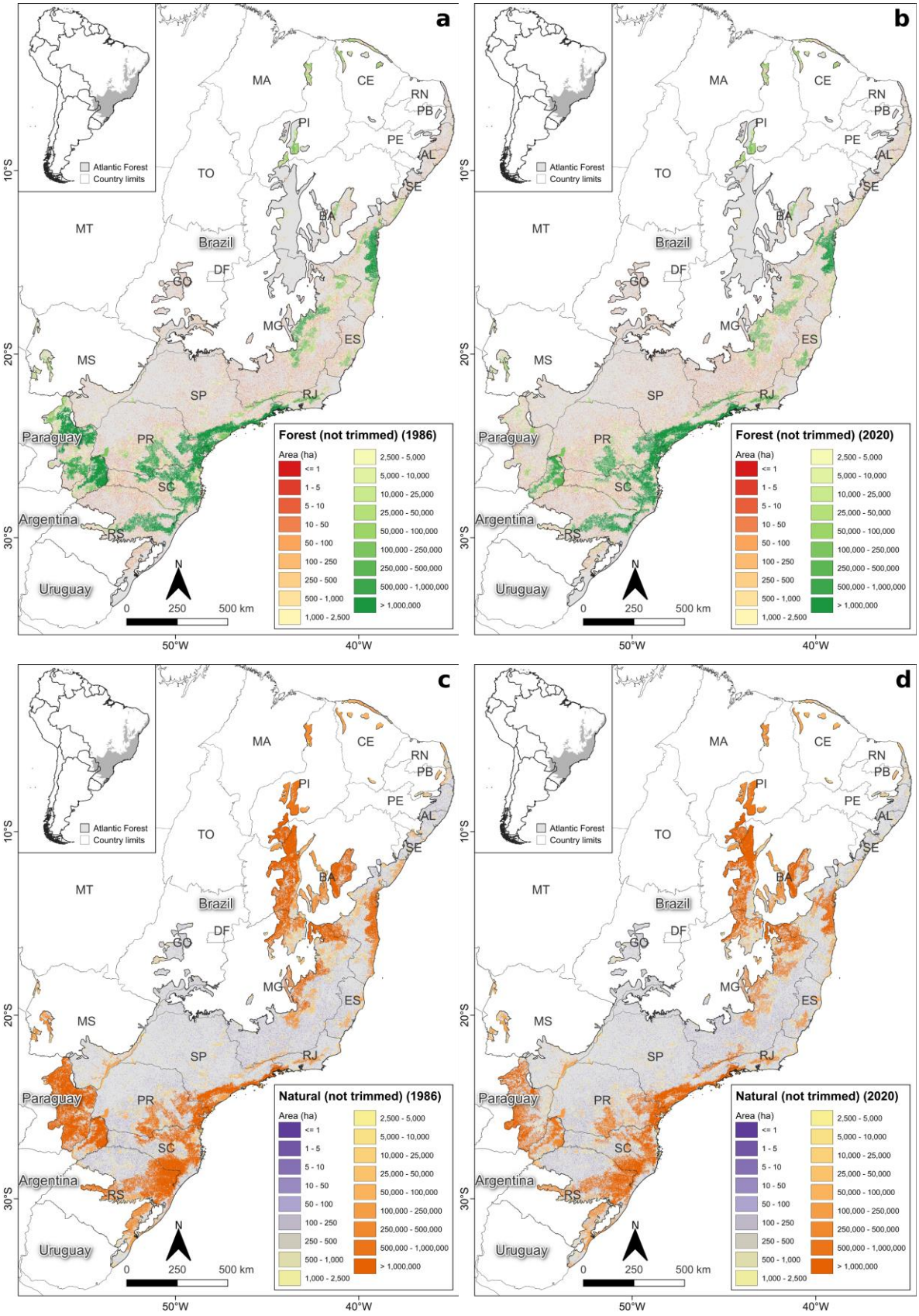


Figure S5. Fragment area for Forest Vegetation (FV) in 1986 (a) and 2020 (b), and for Natural Vegetation (NV) in 1986 (c) and 2020 (d), not trimmed by roads and railways for the entire AF.

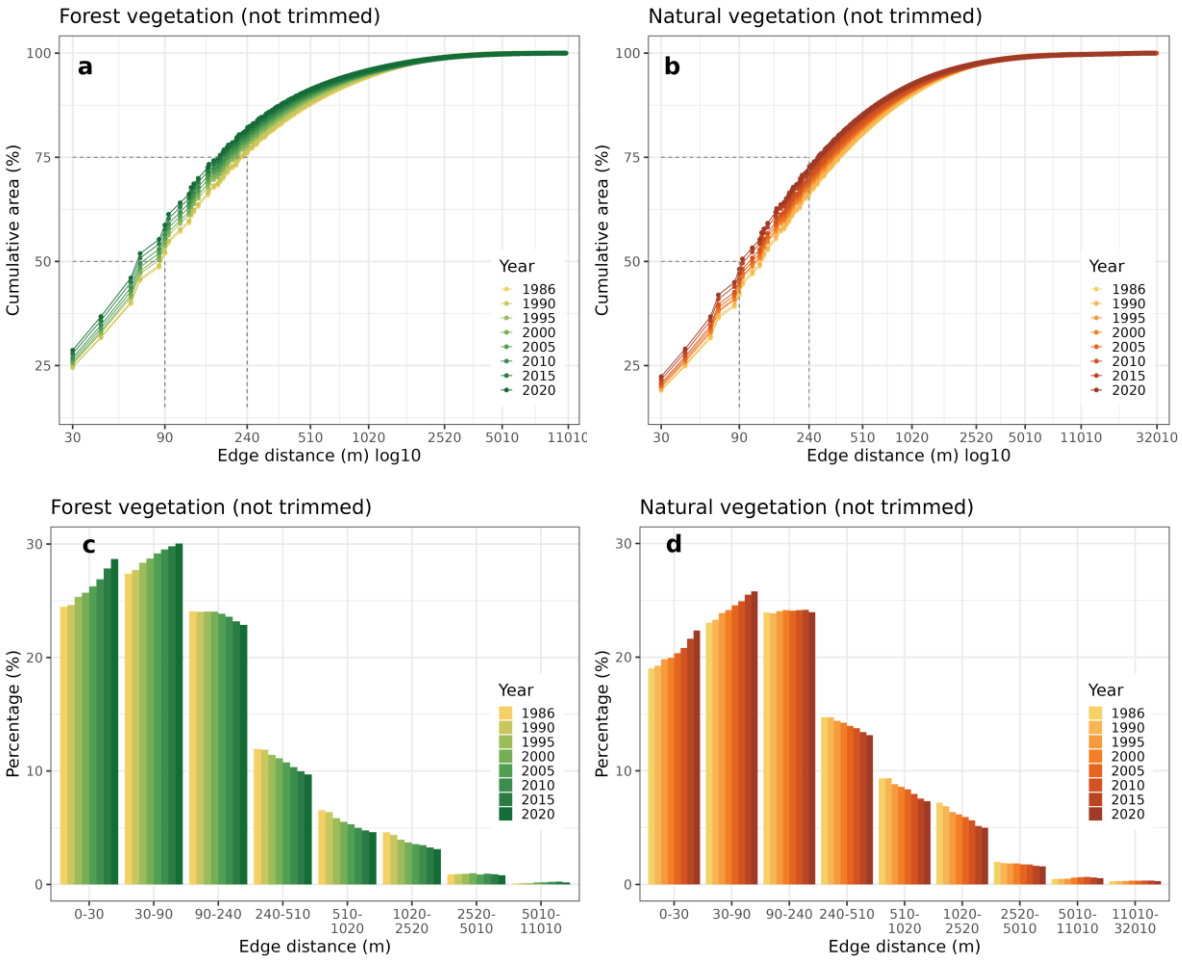


Figure S6. Cumulative (a-b) and per class (c-d) area under edge effect at different edge depths for the Forest Vegetation (FV) and Natural Vegetation (NV) in Atlantic Forest not trimmed by roads and railways.

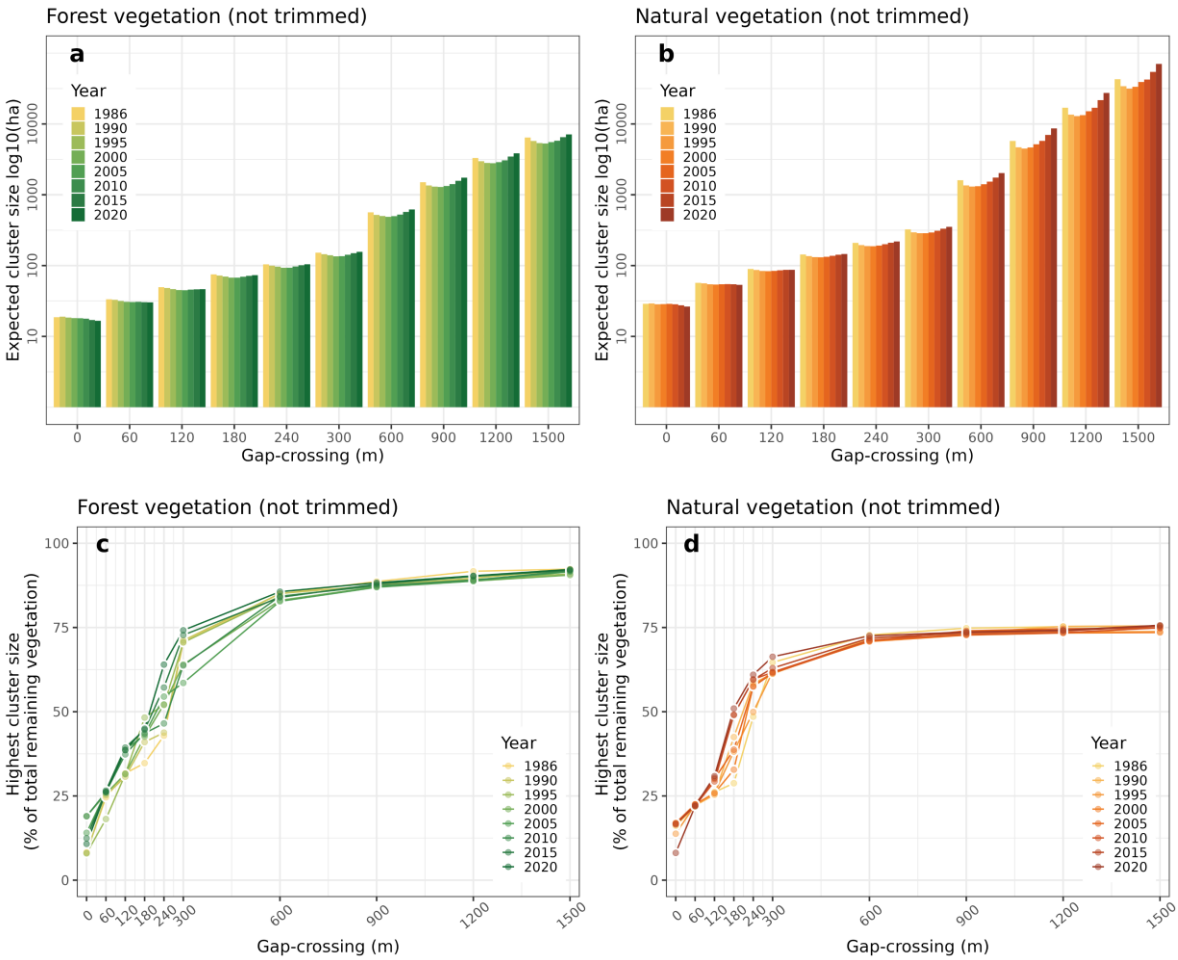


Figure S7. Expected cluster size (a-b) (average functional size; ha) of functionally connected fragments of Forest Vegetation (FV) and Natural Vegetation (NV) for different functional distances values (meters) for the Atlantic Forest. Highest functionally connected forest cluster (c-d) (% of total of FV and NV) estimated across varying functional distances (m), for the Atlantic Forest not trimmed by roads and railways.

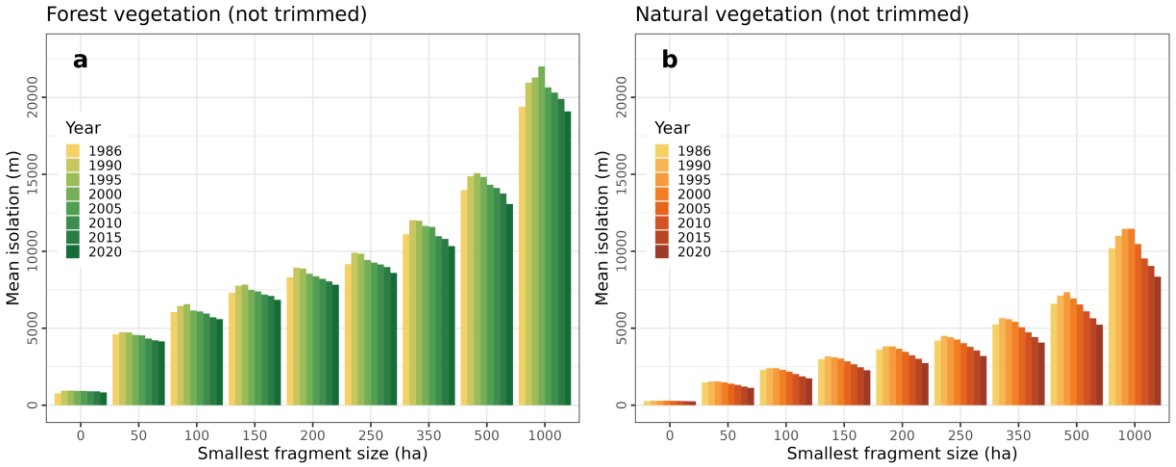


Figure S8. Influence of the smallest fragment size (ha) on the mean isolation (m) between fragments of Forest Vegetation (FV) and Natural Vegetation (NV) for the Atlantic Forest: mean isolation (a-b) not trimmed by roads and railways. Smallest fragments size: 0 ha (all fragments), 50 ha, 100 ha, 150 ha, 200 ha, 250 ha, 350 ha, 500 ha, and 1000 ha.

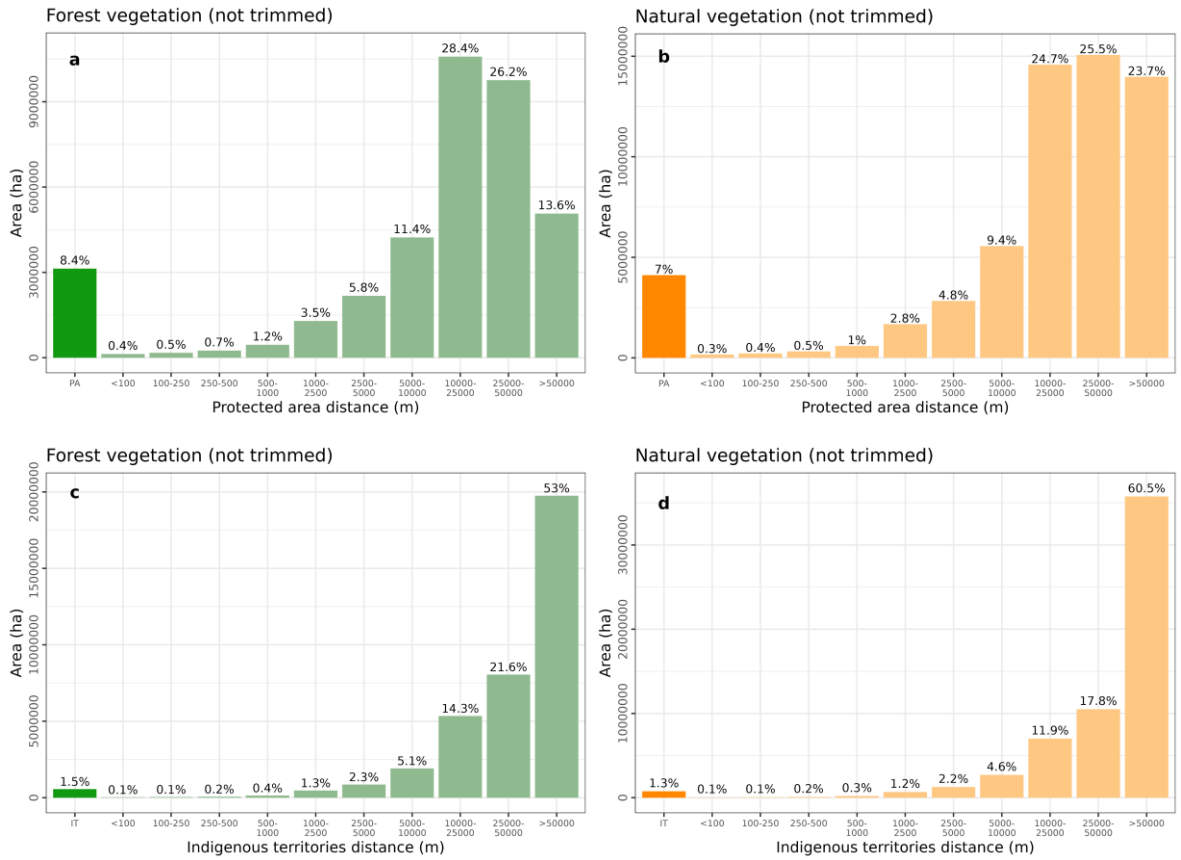


Figure S9. Amount of AF vegetation not trimmed by roads and railways (area and percentage) and their distance from protected areas (PA; a – FV and b – NV) and indigenous territories (IT; c – FV and d – NV) per class.

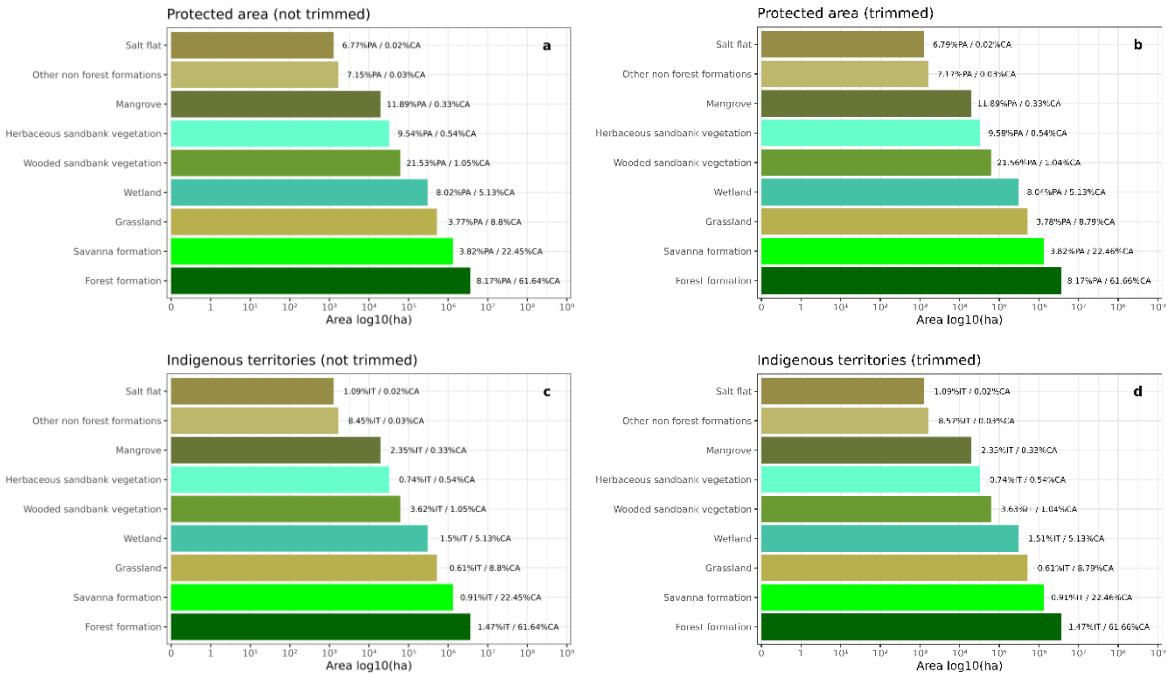


Figure S10. Amount of vegetation by classes for Forest Vegetation (FV) and Natural Vegetation (NV) (area and percentage) within protected areas (PA) (a-b) and indigenous territories (TI) (c-d) for the Atlantic Forest not trimmed and trimmed by roads and railways. %PA: percentage of class area inside PA in relation to the total area of the class; %IT: percentage of class area inside IT in relation to the total area of the class; %CA: percentage of the class area in relation to the total area of vegetation for PA and IT.

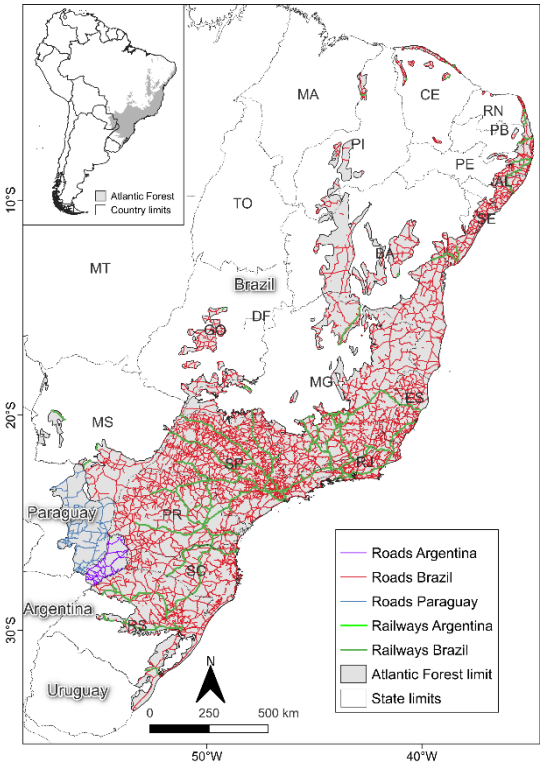


Figure S11. Roads and railways used to trim the Forest Vegetation (FV) and Natural vegetation (NV) fragments.

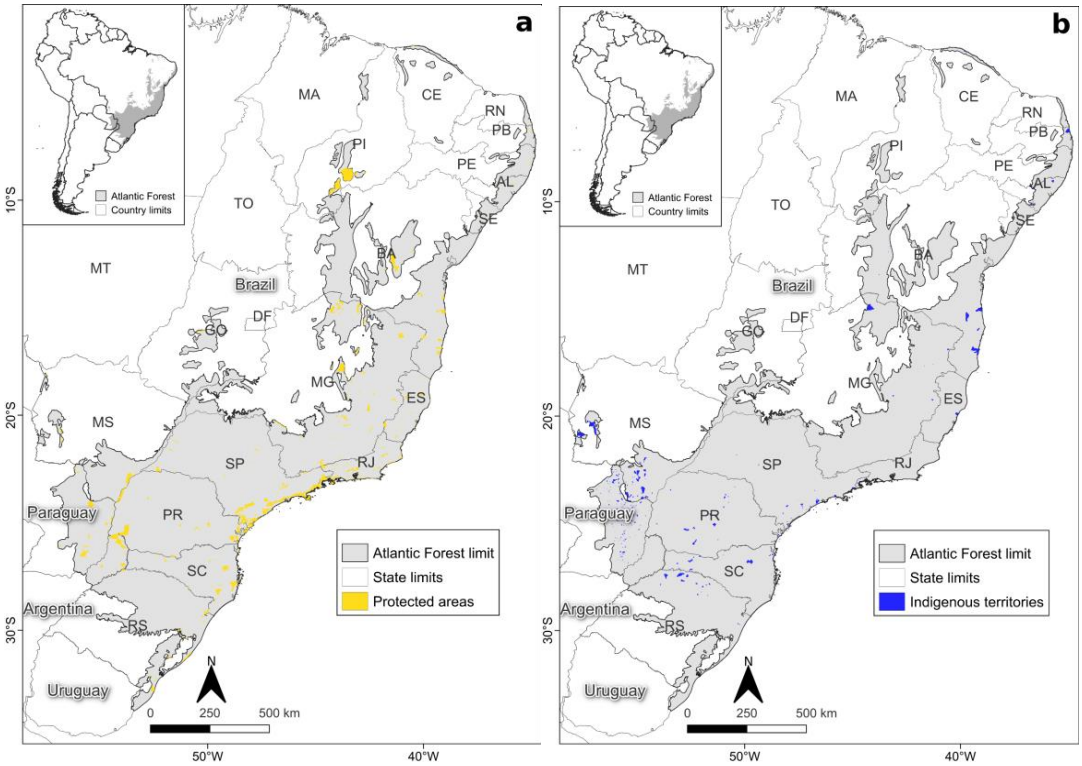
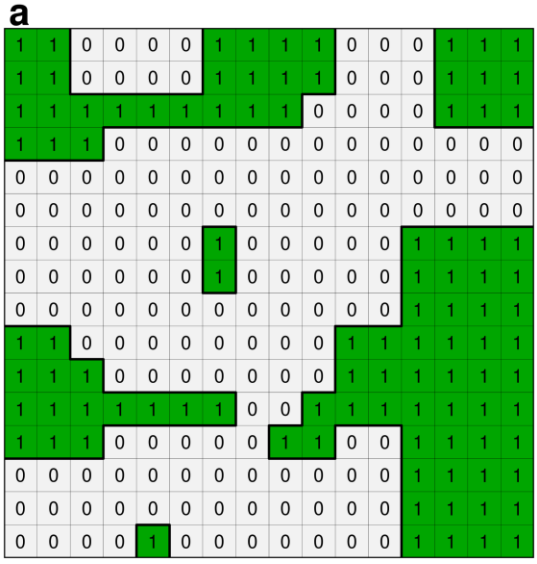


Figure S12. Protected areas (a) and indigenous territories (b) within the Atlantic Forests of South America.

a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1 1 0 0 0 0 1 1 1 1 0 0 0 1 1 1
1 1 1 1 1 1 1 1 1 0 0 0 0 1 1 1
1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
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0 0 0 0 0 0 1 0 0 0 0 0 1 1 1 1
0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1
1 1 0 0 0 0 0 0 0 0 1 1 1 1 1 1
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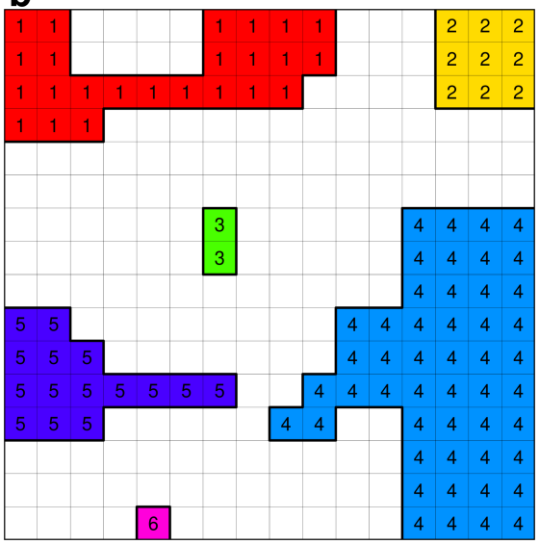
1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1
1 1 1 0 0 0 0 0 1 1 0 0 1 1 1 1
0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1
0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1
0 0 0 0 1 0 0 0 0 0 0 0 1 1 1 1

b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1 1 1 1 1 1 2 2 2
1 1 1 1 1 1 1 1 1 2 2 2
1 1 1
3
3
4 4 4 4
4 4 4 4
4 4 4 4
5 5 4 4 4 4 4 4
5 5 5 4 4 4 4 4 4
5 5 5 5 5 5 5 4 4 4 4 4 4 4
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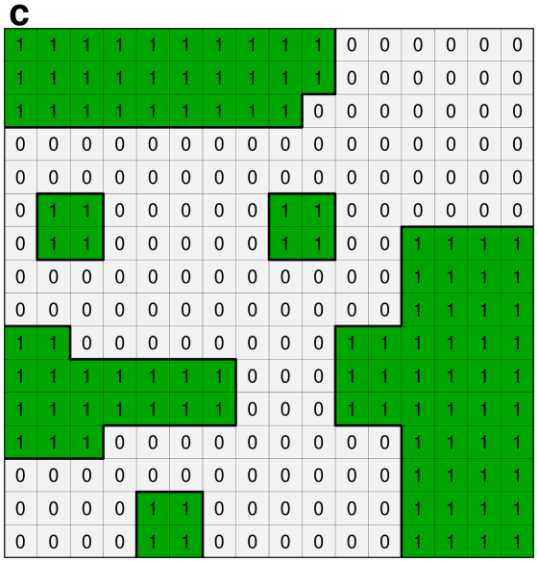
4 4 4 4
4 4 4 4
6 4 4 4 4

c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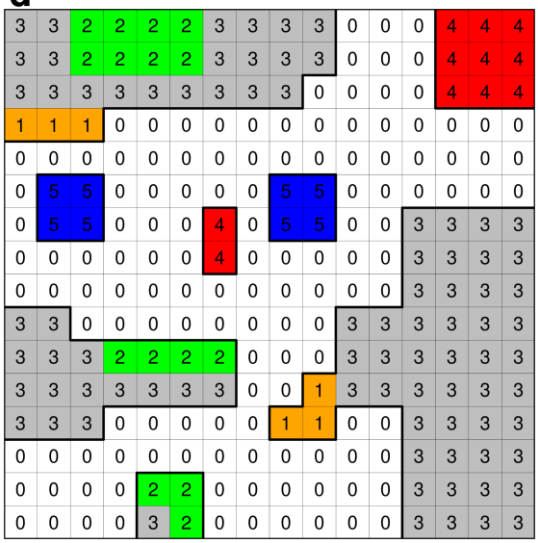
d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0 0 0 0 0 0 0 0 0 0 0 0 3 3 3 3
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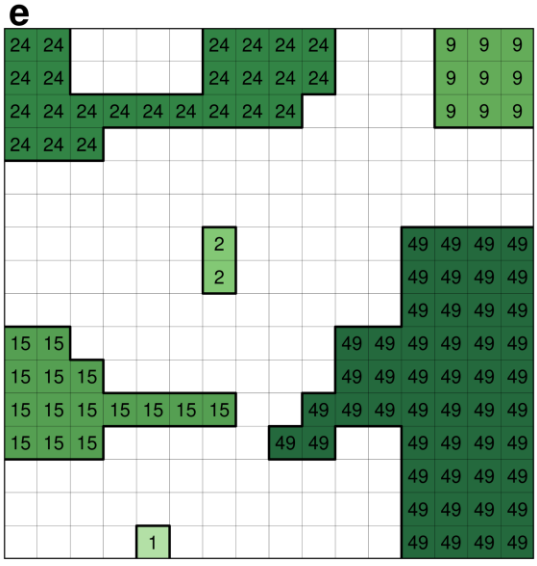
e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24 24 24
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2 49 49 49 49
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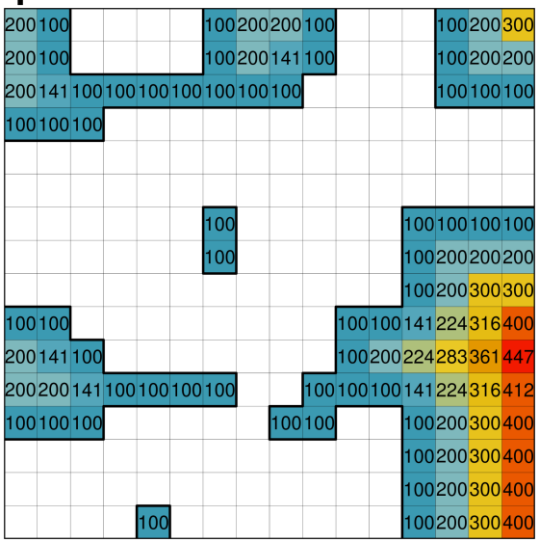
f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100 100 100
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100 200 300 400

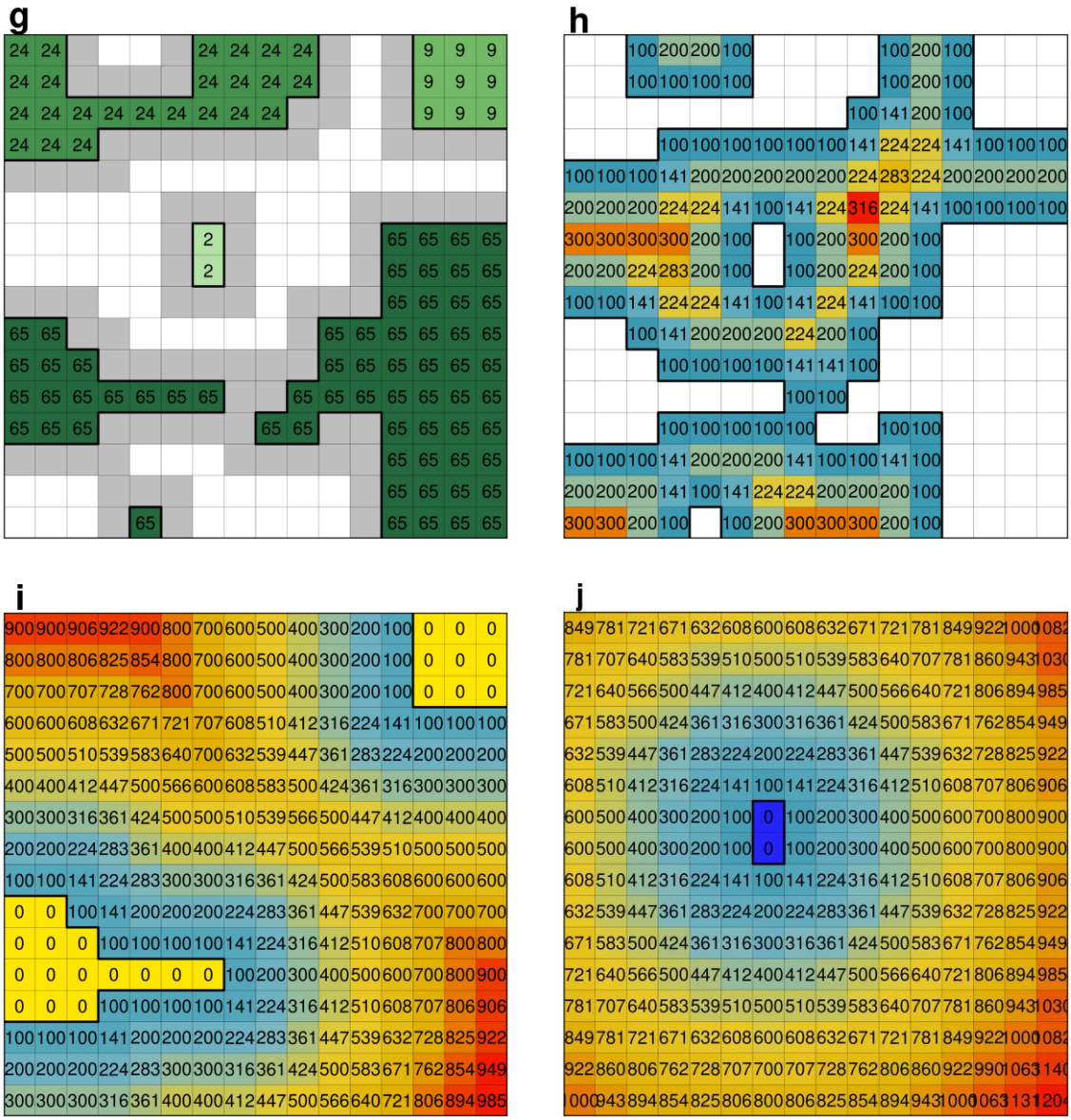

Figure S13. Illustration exemplifying the landscape metrics used to analyze the landscape structure of the AF. Here, the rasters have 100 m of spatial resolution. (a) toy landscape containing binary forest and non-forest data, (b) number of fragments; (c) second toy landscape representing a second moment in time, for the same area; (d) temporal fragment analysis—matrix (0), loss area (1), gain area (2), stable area (3), loss fragment (4), gain fragment (5); (e) fragment size; (f) edge area; (g) functional connectivity; (h) isolation; (i) distance from protected areas; and (j) distance from indigenous territories.

Tables

Table S1. Atlantic Forest (AF) delimitations used to compose the AF "integrated delimitation" adapted from Muylaert et al. (2018).

Reference	Country	Area (ha)	Percentage in relation to Muylaert et al. (2018)	Figure
Muylaert et al. (2018)	Argentina, Brazil, and Paraguay	162,742,129	100.00%	Fig. S1a
Muylaert et al. (2018)	Argentina	2,668,855	1.64%	Fig. S1a
Muylaert et al. (2018)	Brazil	151,470,253	93.07%	Fig. S1a
Muylaert et al. (2018)	Paraguay	8,603,022	5.29%	Fig. S1a
Atlantic Forest Law (2006)	Brazil	128,779,574	79.13%	Fig. S1b
Da Silva and Casteleti (2003)	Brazil	136,422,859	83.83%	Fig. S1c
IBGE (2004)	Brazil	111,751,193	68.67%	Fig. S1d
IBGE (2019)	Brazil	110,656,961	68.00%	Fig. S1e
Dinerstein et al. (2017)	Argentina, Brazil, and Paraguay	134,386,512	82.58%	Fig. S1f

Table S2. Land use and land cover and MapBiomas class code used to compose the "Forest Vegetation" (FV) and "Natural Vegetation" (NV).

Vegetation class	Land use and land cover class	Land use and land cover class abbreviation	MapBiomas class code
Forest Vegetation (FV)	Forest Formation	FF	3
	Mangrove	MG	5
	Wooded Sandbank Vegetation (*restinga*)	WS	49
Natural Vegetation (NV)	Forest Formation	FF	3
	Savanna Formation	SF	4
	Mangrove	MG	5
	Wooded Sandbank Vegetation (*restinga*)	WS	49
	Wetland	WT	11
	Grassland	GL	12
	Salt Flat	ST	32
	Herbaceous Sandbank Vegetation	HS	50
	Other Non-Forest Formations	OF	13

Table S3. Landscape and topographic metrics used to analyze the structure of the landscapes of the AF.

Metric	Description	Class
Number of fragments and fragment size.	Number of fragments, fragment size and percentage of habitat cover for different size classes.	fragment size classes (ha): <1, 1–5, 5–10, 10–50, 50–100, 100–250, 250–500, 500–1000, 1000–2500, 2500–5000, 5000–10000, 10000–25000, 25000–50000, 50000–100000, 100000–250000, 250000–500000, 500000–1000000, and >1000000.
Temporal dynamics of the landscape: area and number of fragments.	Areas of increase, reduction, and stability of fragments that remained throughout time, and area and number of fragments that disappeared and appeared.	Values (Fig. S13): accounting area of loss (1), gain (2), and stable (3) of the stains that remained; number and area of fragments that disappeared (4) and appeared (5).
Edge area.	Percentage of habitat area submitted to edge effects for different edge widths.	Edge widths (m) (pixel size): <30, 30–90, 90–240, 240–510, 510–1020, 1020–2520, 2520–5010, 5010–11010, and 11010–32010.
Functional connectivity.	Area of functionally connected fragments, considering different distance rules for fragment linkage.	Gap-crossing (m) (pixel size): 0, 60, 120, 180, 240, 300, 600, 900, 1200, and 1500.
Mean isolation.	Mean isolation to the nearest habitat fragment. To analyze the effect of small fragments in estimating isolation, the smallest fragments were successively removed.	Size of the small fragments removed (ha): 0 (i.e., no fragments removed), <50, <100, <150, <200, <250, <350, <500, and <1000.
Distance from Protected Areas and Indigenous Territories.	Distance of any given habitat pixel to the nearest Protected Area and Indigenous Territories.	Distance classes (m): 0 (i.e., inside a Protected Area or Indigenous Territories), <100, 100–250, 250–500, 500–1000, 1000–2500, 2500–5000, 5000–10000, 10000–25000, 25000–50000, and >50000.

Table S4. Amount of Forest Vegetation (FV) and Natural Vegetation (NV) for the entire Atlantic Forest between 1986 and 2020, trimmed and not trimmed by roads and railways. For each year and vegetation scenario, the following values are presented: total percentage, number of fragments, and descriptive statistics (average, standard deviation, median and maximum) in hectares.

Year	Scenario	Total percentage (%)	Number of fragments	Total area (ha)	Average area (ha)	Standard deviation area (ha)	Median area (ha)	Maximum area (ha)
1986	FV not trimmed	25.27	2,201,796	41,132,358	18.68	3,687.16	1.35	3,397,448
1986	FV trimmed	25.25	2,230,823	41,096,215	18.42	1,196.23	1.35	416,943
1986	NV not trimmed	39.88	2,251,224	64,909,217	28.83	9,244.66	1.17	10,490,715
1986	NV trimmed	39.84	2,301,462	64,832,338	28.17	2,914.69	1.17	2,711,898
1990	FV not trimmed	24.07	2,059,724	39,164,420	19.01	3,471.66	1.44	3,158,986
1990	FV trimmed	24.04	2,087,132	39,129,892	18.75	1,126.88	1.44	368,668
1990	NV not trimmed	38.39	2,136,171	62,471,881	29.24	9,276.57	1.26	10,532,927
1990	NV trimmed	38.34	2,185,719	62,396,878	28.55	2,897.54	1.26	2,677,168
1995	FV not trimmed	23.24	2,051,750	37,825,688	18.44	3,335.85	1.44	3,007,756
1995	FV trimmed	23.22	2,080,368	37,791,014	18.17	1,059.64	1.44	371,73
1995	NV not trimmed	37.38	2,137,418	60,831,540	28.46	7,985.11	1.26	8,386,742
1995	NV trimmed	37.33	2,188,451	60,756,569	27.76	2,852.16	1.26	2,714,043
2000	FV not trimmed	22.54	2,024,772	36,688,790	18.12	5,091.89	1.44	6,959,510
2000	FV trimmed	22.52	2,052,850	36,655,032	17.86	1,046.31	1.44	414,842
2000	NV not trimmed	36.78	2,091,472	59,861,952	28.62	8,774.22	1.35	10,157,618
2000	NV trimmed	36.74	2,143,251	59,785,947	27.89	2,771.26	1.35	2,662,722

2005	FV not trimmed	22.28	2,009,506	36,260,960	18.04	4,020.41	1.53	5,095,019
2005	FV trimmed	22.26	2,039,470	36,225,545	17.76	1,010.36	1.44	417,447
2005	NV not trimmed	36.47	2,060,924	59,344,869	28.8	8,663.39	1.35	10,017,365
2005	NV trimmed	36.42	2,114,462	59,266,367	28.03	2,717.01	1.35	2,603,116
2010	FV not trimmed	22.44	2,052,341	36,522,265	17.8	5,034.37	1.44	6,937,266
2010	FV trimmed	22.42	2,085,081	36,484,677	17.5	992.08	1.44	420,824
2010	NV not trimmed	36.45	2,085,299	59,314,001	28.44	8,356.43	1.35	9,792,496
2010	NV trimmed	36.4	2,142,906	59,232,500	27.64	2,658.21	1.35	2,625,471
2015	FV not trimmed	22.65	2,161,797	36,867,412	17.05	3,705.34	1.44	4,582,605
2015	FV trimmed	22.63	2,199,621	36,826,224	16.74	986.36	1.35	406,818
2015	NV not trimmed	36.36	2,151,325	59,180,724	27.51	8,195.2	1.35	9,895,304
2015	NV trimmed	36.31	2,215,391	59,095,705	26.68	2,534.84	1.26	2,532,163
2020	FV not trimmed	22.89	2,244,015	37,251,477	16.6	3,343.34	1.35	4,010,367
2020	FV trimmed	22.86	2,288,052	37,206,124	16.26	941.46	1.35	427,557
2020	NV not trimmed	36.32	2,241,089	59,110,442	26.38	6,103.28	1.26	4,779,875
2020	NV trimmed	36.27	2,311,098	59,022,554	25.54	2,370.81	1.26	2,120,105

Table S5. Forest Vegetation (FV) and Natural Vegetation (NV) for different AF delimitations for the year of 2020, trimmed and not trimmed by roads and railways. For each delimitation and vegetation scenario are presented: vegetation percentage, number of fragments, and total and average area in hectares. The AF delimitations can be seen in Fig. S1.

AF delimitation	Scenario	Vegetation percentage (%)	Number of fragments	Total area (ha)	Average area (ha)
Atlantic Forest Law (2006)	FV not trimmed	24.07	1,788,188	30,992,081	17.33
Atlantic Forest Law (2006)	FV trimmed	24.03	1,827,401	30,951,902	16.94
Atlantic Forest Law (2006)	NV not trimmed	35.98	1,835,652	46,333,549	25.24
Atlantic Forest Law (2006)	NV trimmed	35.93	1,892,424	46,264,910	24.45
Da Silva and Casteleti (2003)	FV not trimmed	23.18	1,902,365	31,622,147	16.62
Da Silva and Casteleti (2003)	FV trimmed	23.15	1,944,181	31,579,924	16.24
Da Silva and Casteleti (2003)	NV not trimmed	34.36	1,933,978	46,875,495	24.24
Da Silva and Casteleti (2003)	NV trimmed	34.31	1,993,586	46,806,307	23.48
IBGE (2004)	FV not trimmed	26.06	1,641,173	29,122,577	17.74
IBGE (2004)	FV trimmed	26.02	1,679,755	29,083,232	17.31
IBGE (2004)	NV not trimmed	31.84	1,671,550	35,586,103	21.29
IBGE (2004)	NV trimmed	31.79	1,722,521	35,529,740	20.63
IBGE (2019)	FV not trimmed	26.50	1,649,485	29,326,354	17.78
IBGE (2019)	FV trimmed	26.47	1,688,416	29,286,696	17.35
IBGE (2019)	NV not trimmed	31.50	1,662,346	34,859,089	20.97
IBGE (2019)	NV trimmed	31.45	1,711,603	34,805,010	20.33
Dinerstein et al. (2017)	FV not trimmed	25.06	1,796,063	32,173,468	17.91
Dinerstein et al. (2017)	FV trimmed	25.03	1,929,003	33,637,977	17.44
Dinerstein et al. (2017)	NV not trimmed	37.04	1,767,078	40,934,679	23.17
Dinerstein et al. (2017)	NV trimmed	36.99	1,976,891	49,709,385	25.15

Table S6. Dynamics of the landscape for the entire Atlantic Forest, from 1986-2005 and from 2005-2020 for two scenarios: not trimmed and trimmed. Balance of total area represents the subtraction of area gained minus area lost. Balance of total area (%) is in terms of percentage in relation to the total AF area. Balance of number of fragments represents the subtraction of the number of fragments gained minus the number of fragments lost. Mean size of fragments gained (ha), and mean size of fragments lost (ha) represent the average size of fragments gained and lost. The table with all measures is presented in Table S3.

Period	Scenario	Balance of total area (ha)	Balance of total area (%)	Balance of number of fragments	Mean size of fragments gained (ha)	Mean size of fragments lost (ha)
1986-2005	FV not trimmed	-4,871,398	-2.99	242,715	1.14	1.35
1986-2005	FV trimmed	-4,870,670	-2.99	242,757	1.12	1.33
1986-2005	NV not trimmed	-5,564,348	-3.42	227,621	1.11	1.21
1986-2005	NV trimmed	-5,565,971	-3.42	226,812	1.08	1.20
2005-2020	FV not trimmed	990,517	0.61	373,616	1.08	0.97
2005-2020	FV trimmed	980,579	0.60	385,783	1.06	0.96
2005-2020	NV not trimmed	234,427	-0.14	301,911	1.06	0.96
2005-2020	NV trimmed	243,813	-0.15	314,047	1.03	0.94

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CAPÍTULO 2: ATLANTIC SPATIAL: a data set of landscape, topographic, hydrological, and anthropic metrics for the Atlantic Forests of South America

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Tipo de manuscrito: Data paper

(SUBMETIDO E EM REVISÃO NA REVISTA “ECOLOGY” EM 20 DE NOVEMBRO DE 2023)

ATLANTIC SPATIAL: a data set of landscape, topographic, hydrological, and anthropic metrics for the Atlantic Forest

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Open Research statement

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Introduction

In ecology, space matters. Space affects the main drivers of biodiversity, since it regulates the underlying processes affecting the distribution and dynamics of species (Fletcher and Fortin 2018). These ecological processes, such as environmental filtering, biotic interactions, dispersal and ecological drift drive the response of organisms to environmental factors such as climate, topography, land use and land cover (LULC), soil types and habitat connectivity and heterogeneity (Anderle et al. 2022, Messager et al. 2023). Thus, space is a fundamental component in the face of rapid effects of climate and LULC changes at local and global scales, as well as their widespread consequences for habitat loss and fragmentation (Jetz et al. 2007, He et al. 2019, Williams and Newbold 2020). Having available geospatial environmental data is essential to assess these effects at different spatial and temporal scales, extents and grains (e.g., Lima-Ribeiro 2015, Vega et al. 2017, Fick and Hijmans 2017, Souza et al. 2020, Karger et al. 2020, Poggio et al. 2021, Potapov et al. 2022, Hawker et al. 2022, Hansen et al. 2022, Tang and Werner 2023). Comprehensive spatial data sets are important to address conservation and restoration efforts to maintain biodiversity and their ecological processes (Dirzo et al. 2014, He et al. 2015, Young et al. 2016, Johnson et al. 2017). Ultimately, such data sets would help to unravel frequent 'spatial complications' [neglected contribution of space in explaining ecological processes] (Kareiva 1994) in ecology and other geospatial disciplines.

Habitat loss and fragmentation are currently the major threats to biodiversity and ecological processes worldwide (Fahrig 2003, Haddad et al. 2015). Landscapes composition and configuration are essential factors determining biodiversity, population dynamics, species interactions, dispersal and movement, functions the biota perform across the space (Fahrig 2003, Driscoll et al. 2013, Duflot et al. 2017). Besides, different landscape metrics can be used as proxies of landscape heterogeneity to predict biodiversity and ecosystem function (Tonetti et al. 2023). This is especially relevant in fragmented landscapes where natural vegetation fragments are surrounded by different anthropic land cover types (Fischer and Lindenmayer 2007, Turner and Gardner 2015). Landscape metrics can also be used in the identification of priority areas for conservation (Tambosi et al. 2014), in addition to predicting species' potential distribution (Fletcher et al. 2016). Furthermore, these metrics must be computed considering different scales depending on the phenomenon of interest (Jackson and Fahrig 2015, Miguet et al. 2016), and the specific species functional responses to landscape structure (Mimet et al. 2013, Riva and Nielsen 2020).

The Atlantic Forest of South America (AF) is among the global biodiversity hotspots due to its high species richness and endemism associated with severe habitat loss (Myers et al. 2000, Sloan et al. 2014). The AF covers almost the entire coast of Brazil and reaches inland portions of the continent in parts of Paraguay and Argentina, and its vegetation covered over 1.6 million km^2 before the European colonization (Marques et al. 2021). Due to its wide longitudinal, latitudinal and altitudinal range, the AF has high environmental heterogeneity with different vegetation types generated mainly by the rainfall distribution, from its coast as Mangrove and Sandy coastal plain vegetation (*restinga*), passing through humid forest (Dense Ombrophilous, Open Ombrophilous, Mixed Ombrophilous), and dry forest formations (Semideciduous and Deciduous Seasonal) (Joly et al. 2014). These geographical characteristics, combined with a large topographic variability and pre-historic process of formation, favored high species diversification rates and endemism (Carnaval et al. 2014, Peres et al. 2020).

The high diversification rate in AF is evidenced by its high biodiversity: it contains almost 18,000 species of plants (Flora e Funga do Brasil 2023); 2,645 species of Tetrapoda (Figueiredo et al. 2021); around 1,000 species of fish (Reis et al. 2016); 1400 species of social insects (Feitosa et al. 2021); more than 2,000 species of butterflies (Iserhard et al. 2017); more than 112,000 species of arachnids (Giupponi et al. 2017); and from 3 to 12 million species of unknown bacteria (Lambais et al. 2006). In addition to its high biodiversity, the AF directly provides ecosystem services for >150 million people, such as water provisioning and regulation, hydroelectric energy generation, food production, pollination, soil protection, climate regulation, carbon storage, air quality and cultural services (Joly et al. 2014, Pires et al. 2021). A great part of the AF biodiversity is highly threatened, especially birds (Bonfim et al. 2021), small mammals (Palmeirim et al. 2019), medium and large mammals (Rios et al. 2021b) and amphibians (Almeida-Gomes and Rocha 2014). Furthermore, ecological processes are also affected by landscape modifications, such as interaction networks (Marjakangas et al. 2020, Monteiro et al. 2022), carbon storage (Bello et al. 2015, de Lima et al. 2020, Pyles et al. 2022) and pollination (Varassin et al. 2021). In addition, other threats to the AF landscapes are defaunation (Galetti et al. 2017, 2021), the introduction of non-native species (Vitule et al. 2021) and climate change (Scarano and Ceotto 2015, Vale et al. 2021).

The AF covers the three countries (Argentina, Brazil and Paraguay) with the largest deforestation areas in the world between 1982 and 2016 (Song et al. 2018). Thus, landscape modifications within the AF have caused impacts reported by a series of studies that still show a warning scenario. Despite a temporal stability of around 28 Mha of forest, a considerable part of this forest is made up of the replacement of old native forests by young forests (Rosa et al.

2021). Furthermore, although recent estimates state that there are around about 23% of forest and 36% of natural vegetation, there is a high fragmentation scenario—97% of fragments are <50 ha, 60% are under edge effect (<90 m), and there is high isolation of vegetation fragments (mean of 250 to 830 m) (Vancine et al. 2024). Moreover, the high density of linear infrastructure (roads and railways) in AF affects the vegetation remnants—especially the large ones (>500,000 ha), proving to have a major negative impact on biodiversity (Cassimiro et al. 2023, Vancine et al. 2024).

The AF is one of the most intensely studied biomes in the world. A large initiative organized by Brazilian researchers – the ATLANTIC SERIES of data papers – have compiled hundreds of thousands of records of occurrence and abundance of animal and plant species in the AF (https://esajournals.onlinelibrary.wiley.com/doi/toc/10.1002/(ISSN)1939-9170.AtlanticPapers). Biodiversity data were collected for decades and have been recently synthesized for AF in numerous data papers from the collection (Bello et al. 2017, Bovendorp et al. 2017, Figueiredo et al. 2017, Lima et al. 2017, Muylaert et al. 2017, Gonçalves et al. 2018a, 2018b, Hasui et al. 2018, Vancine et al. 2018, Santos et al. 2018, Souza et al. 2019, Culot et al. 2019, Ramos et al. 2019, Rodrigues et al. 2019, Silva et al. 2022, Boscolo et al. 2023). These data sets have provided an unprecedented opportunity for the assessment of how environmental conditions and species interactions can predict biodiversity patterns from species to assemblages (e.g. Bovendorp et al. 2019, Palmeirim et al. 2019, Rios et al. 2021b, 2021a, Bonfim et al. 2021). However, such studies rely on a highly variable set of spatial data and require intensive data processing, usually differing in the scale and grain, as well as source and quality.

Here, we present the ATLANTIC SPATIAL data set, where we organize and synthesize spatial data on land cover and land use, landscape, topographic, hydrological, and anthropic metrics for the entire AF. Making these data available avoids complex and computationally demanding geoprocessing steps from having to be re-run and allows for different biodiversity studies to be more reproducible and potentially comparable, since they would use as source the same set of spatial data. We present raster maps at 30-m resolution, making it possible to easily integrate spatial and biodiversity data in ecological studies. We provide several metrics derived from different moving window sizes, so that it can be used as effect scales on multiple scale analyses (Jackson and Fahrig 2015). Our aim is to facilitate the use of these layers in a series of studies, within fields such as landscape ecology (Beca et al. 2017, Regolin et al. 2017, Marjakangas et al. 2020, Monteiro et al. 2022), species distribution modeling (SDMs) (Ferro e Silva et al. 2018, Bertassoni et al. 2019, Santos et al. 2020, 2022, Oshima et al. 2021, Tonetti

et al. 2022), spatial prioritization (Tambosi et al. 2014, Rosa et al. 2021, Iezzi et al. 2022, Tonetti et al. 2023) and habitat restoration (Melo et al. 2013, Pinto et al. 2014, 2014, Zwiener et al. 2017, Lopes et al. 2022, Piffer et al. 2022, Schweizer et al. 2022, Zupo et al. 2022, Bicudo da Silva et al. 2023). We hope this information enables the integration of biodiversity and environmental data for the AF in ecological studies and expect it to be a common reference to be used as a basis for landscape planning, biodiversity conservation and forest restoration programs.

METADATA

Class I. Data set descriptors

A. Data set identity

Title: ATLANTIC SPATIAL: a data set of landscape, topographic, hydrological, and anthropic metrics for the Atlantic Forests.

B. Data set identification code

ATLANTIC_SPATIAL.csv

ATLANTIC_SPATIAL.zip

C. Data set description

1. Originators

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2. Abstract

Space is one of the main drivers of biodiversity, once it regulates the underlying processes affecting the distribution and dynamics of species. It is a fundamental factor in face of the rapid

climate and land use and land cover changes at local and global scales, which are linked to habitat loss and fragmentation and their impacts on various organisms. The Atlantic Forest of South America (AF) is among the global biodiversity hotspots because of its high species richness and endemism. Most of the threats to the AF biodiversity is due to the expansion of urbanization and industry, extensive agricultural and livestock production and mining. Here, we make available integrated and fine-scale spatial information (resolution = 30 m) for the entire AF extent for the year 2020. The metrics consider different vegetation classes (forest and forest plus other natural vegetation), effects of linear structure (roads and railways) and multiple scales (radius buffer from 50 m to 2,500 m and up to 10 km for some metrics). The entire data set is composed of 500 rasters and the AF delimitation vector, available through the R package *atlanticr*, which we developed to facilitate the organization and acquisition of the data. The metrics consists of land cover (31 classes), distance to grouped land cover classes (forest vegetation, natural vegetation, pasture, temporary crop, perennial crop, forest plantation, urban areas, mining, and water), a set of landscape, topographic and hydrological metrics, and anthropic infrastructure. The landscape metrics include landscape morphology (classification as matrix, core, edge, corridor, stepping stone, branch, and perforation), fragment area and proportion, area and number of patches, edge and core areas and proportion, structural and functional connectivity (for different organisms' gap-crossing capabilities), distance to fragment edges, fragment perimeter and perimeter-area ratio and landscape diversity. Topographic metrics include elevation, slope, aspect, curvatures, and landform elements (peak, ridge, shoulder, spur, slope, hollow, footslope, valley, pit and flat), hydrological metrics comprise potential springs and its kernel and potential streams and respective distances and anthropic infrastructure maps contain roads, railways, protected areas and indigenous territories and the respective distance to each of them. These data sets will allow for efficient integration of biodiversity and environmental data for the AF in future ecological studies, and we expect it to be an important reference and data source for landscape planning, biodiversity conservation and forest restoration programs.

D. Keywords

Tropical, hotspot, habitat loss, fragmentation, covariates, spatial, rainforest.

Class II. Research origin descriptors

A. Overall project description

1. Identity

A compilation of spatial covariates data of landscape, topographic, hydrological, and anthropic metrics for the entire AF at fine spatial resolution (30-m) for the year 2020.

2. Originators

The ATLANTIC SPATIAL project was coordinated by Maurício H. Vancine and Bernardo Brandão Niebuhr at the São Paulo State University (UNESP), and the data set was assembled with help from all the other authors. This is part of ATLANTIC SERIES, which is led by Mauro Galetti and Milton Ribeiro at the São Paulo State University (UNESP).

3. Period of study

Data were processed for the year 2020.

4. Objectives

The aim of this data paper was to provide a spatial covariates data set of landscape, topographic, hydrological, and anthropic metrics for the entire Atlantic Forest (AF) at fine spatial resolution (30-m) for the year 2020.

5. Abstract

Same as above.

6. Sources of funding

The compilation of this data set was supported by São Paulo Research Foundation (FAPESP) grants #2022/01899-6 (MVH), #2021/02132-8 (JEFO), #2020/11129-8 (EMZ), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) grants fellowships 88887.513979/2020-00 and 1588183 (MVH) and Conselho Nacional do Desenvolvimento Científico e Tecnológico (CNPq) grants #130909/2020-3 (EMZ). BBN is supported by the Research Council of Norway (Grant #287925) and by the NINA basic funding (Research Council of Norway, Grant #160022/F40). RLM is supported by Bryce Carmine and Anne Carmine (née Percival), through the Massey University Foundation. CHG is a research fellow of the National Council for Scientific and Technological Development - CNPq (grant #311209/2021-1). MCR was supported by FAPESP (processes #2013/50421-2, #2020/01779-

5, #2021/08322-3, #2021/08534-0, #2021/10195-0, #2021/10639-5, #2022/10760-1) and CNPq (processes #442147/2020-1, #440145/2022-8, #402765/2021-4, #313016/2021-6, #440145/2022-8) and São Paulo State University - UNESP for their financial support. This study was financed in part by CAPES Brazil – Finance Code 001. This study is also part of the Center for Research on Biodiversity Dynamics and Climate Change, which is financed by FAPESP.

B. Specific subproject description

1. Site description

AF extends from 3ºS to 33ºS, and from 35ºW to 58ºW with ~163 Mha, covering coastal and inland portions of Brazil, Argentina and Paraguay (Marques et al., 2021) (Figure 1). Due to this large extension, the AF boundaries create important ecotones with other vegetation domains such as Cerrado, Caatinga, Chaco and Pampa (Marques et al., 2021). The vegetation from AF is a complex mosaic composed of five main vegetation types—Dense Ombrophilous, Open Ombrophilous, Mixed Ombrophilous, Semideciduous Seasonal and Deciduous Seasonal (Joly et al., 2014). Additionally, the AF also includes mangroves and coastal scrub vegetation (Marques et al., 2021). Furthermore, there are many associated ecosystems such as altitude grasslands (*campos rupestres* and *campos de altitude*), oceanic islands, beaches, rocky shores, dunes, marshes, inland swamps and mountain forest (*brejos de altitude*) in the Northeast region (Scarano, 2002).

2. Experimental or sampling design

None.

3. Research methods

Atlantic Forest delimitation

We used the integrative AF delimitation adapted from Muylaert et al. (2018), a general delimitation encompassing the main proposed delimitations across several associated ecosystems (Muylaert et al. 2018, Cunha et al. 2019, Marques et al. 2021). We adapted this delimitation by merging the following original maps and most recent ones: 1. AF delimitation defined by Brazilian legislation (Federal Decree No. 750/93 and Atlantic Forest Law No. 11,428/2006) named Atlantic Forest Law by IBGE (2018); 2. AF limit defined by (Da Silva and Casteleti 2003); 3. AF delimitation defined by IBGE (2004); 4. AF most recent

delimitation defined by IBGE (2019) and; 5. AF delimitation defined by (Dinerstein et al. 2017) and used in the Ecoregions 2017® (https://ecoregions.appspot.com).

Finally, we adjusted the resulting delimitation for the coastal areas using the Brazilian territorial delimitation from IBGE (https://www.ibge.gov.br) for 2021, to align the limit considering the most current delimitations of mangrove, dunes and sandy coastal plain vegetation (*restinga*) (Scarano 2002). The final delimitation has an area total of 162,742,129 ha, that covers 3653 municipalities from 18 Brazilian states (151,470,253 ha, 93.07%), and parts of Argentina (2,668,855 ha, 1.64%) and Paraguay (8,603,022 ha, 5.29%) (Figure 1).

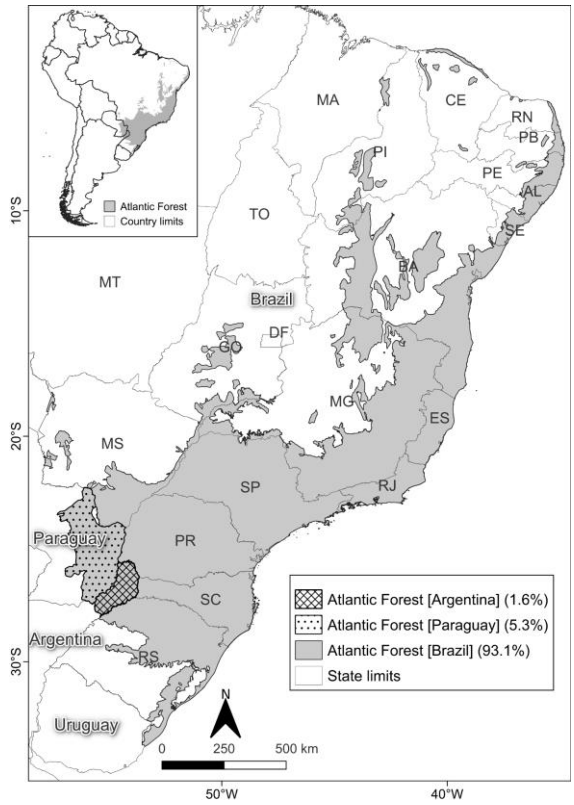


Figure 1. Integrative Atlantic Forest delimitation, adapted from (Muylaert et al. 2018).

Raster resolution and coordinate system

All geospatial data sets were rasterized or adjusted the raster resolution to 30 m (~1.8 billion cells with values). All rasters were reprojected to Albers Conical Equal Area Brazil (SIRGAS 2000) (https://spatialreference.org/ref/sr-org/albers-conical-equal-area-brazil-sirgas-2000) and are therefore presented in meters.

Land use and land cover data

We compiled Land Use and Land Cover (LULC) maps from MapBiomas Brazil

collection 7 (https://mapbiomas.org) and MapBiomas Bosque Atlántico collection 2 (https://bosqueatlantico.mapbiomas.org) (Souza et al. 2020). These data sets reconstruct annual LULC information at the 30-m spatial resolution from 1985 to 2021, based on a pixel-based random forest classifier of Landsat satellite images processed through Google Earth Engine, and with posterior accuracy of 89.8% for the AF (Souza et al. 2020). We considered the LULCs map for 2020 to provide the most recent data that included data validation for the previous year (2019) and subsequent year (2021), guaranteeing better accuracy for the LULC classes.

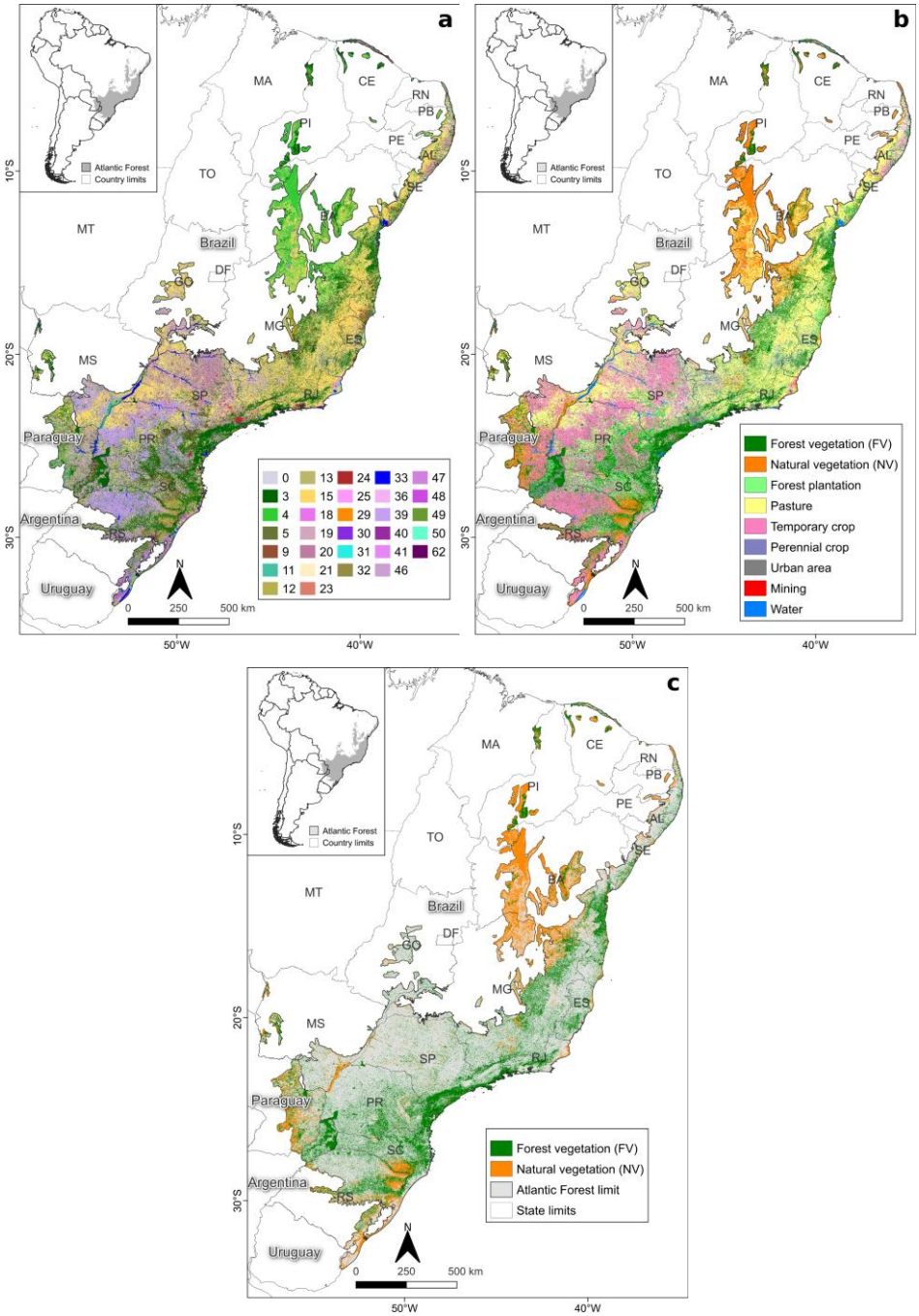


Figure 2. Data framework used to summarize land use land cover (LULC) classes into Atlantic Forest habitat types. (a) The LULC classes refer to MapBiomas in the AF (Brazil, Argentina and Paraguay). (b) Grouped land cover classes. (c) Two vegetation classes were considered as habitat to calculate the landscape metrics. MapBiomas classes are presented in Table 1.

The LULC map from MapBiomas consists of a map with 31 classes (Table 1; Figure 2a). To calculate the distance from land cover classes metrics, we grouped the classes into seven broad categories: pasture, temporary crop, perennial crop, forest plantation, urban areas, mining and water (Table 1; Figure 2b). For the landscape metrics, we defined two vegetation classes for analysis: "Forest Vegetation" (FV), selecting the land cover classes of "Forest" and "Natural Vegetation" (NV), selecting the land cover classes of "Forest" and "Non-Forest Natural Formation" (Table 1; Figure 2c). The only exception for landscape metrics was heterogeneity, for which we used all 31 classes in the calculation.

Table 1. Land use and land cover classes grouped as vegetation classes. The Atlantic Forest spatial maps were based on MapBiomas collection 7.

Land use and land cover class	MapBiomas class code	Grouped land cover classes	Vegetation class
Not specified	0	Not used	Not used
Forest Formation	3	Forest vegetation	Forest vegetation (FV) and Natural vegetation (NV)
Savanna Formation	4	Natural vegetation	Natural vegetation (NV)
Mangrove	5	Forest vegetation	Forest vegetation (FV) and Natural vegetation (NV)
Forest Plantation	9	Forest plantation	Not used
Wetland	11	Natural vegetation	Natural vegetation (NV)
Grassland	12	Natural vegetation	Natural vegetation (NV)
Other non-Forest Formations	13	Natural vegetation	Natural vegetation (NV)
Pasture	15	Pasture	Not used

Temporary Crop	19	Temporary crop	Not used
Sugar cane	20	Temporary crop	Not used
Mosaic of Uses	21	Not used	Not used
Non vegetated area	22	Not used	Not used
Beach, Dune and Sand Spot	23	Not used	Not used
Urban Area	24	Urban area	Not used
Other non-Vegetated Areas	25	Not used	Not used
Rocky Outcrop	29	Not used	Not used
Mining	30	Mining	Not used
Aquaculture	31	Not used	Not used
Salt Flat	32	Natural vegetation	Natural vegetation (NV)
River, Lake and Ocean	33	Water	Not used
Perennial Crop	36	Perennial crop	Not used
Soybean	39	Temporary crop	Not used
Rice	40	Temporary crop	Not used
Other Temporary Crops	41	Temporary crop	Not used
Coffee	46	Perennial crop	Not used
Citrus	47	Perennial crop	Not used
Other Perennial Crops	48	Perennial crop	Not used
Wooded Sandbank Vegetation	49	Forest vegetation	Forest vegetation (FV) and Natural vegetation (NV)
Herbaceous Sandbank Vegetation	50	Natural vegetation	Natural vegetation (NV)
Cotton	62	Temporary crop	Not used

We used linear infrastructure (roads and railways) to trim FV and NV areas overlapping with these structures. This way we avoided overestimating large fragments, since roads can decrease the connectivity of large patches (Martinez Pardo et al. 2023) and for different taxa (Cassimiro et al. 2023). Roads and railways data were downloaded from official geospatial databases for the three countries: Brazil (Instituto Brasileiro de Geografia e Estatística – IBGE; IBGE, 2021; https://www.ibge.gov.br), Argentina (Instituto Geográfico

Nacional – IGN; IGN, 2022; https://www.ign.gob.ar) and Paraguay (Instituto Nacional de Estadística – INE; INE, 2022; https://www.ine.gov.py). The data summed 14,072 km of railways and 125,483 km of roads, with a total of 139,554 km (Figure 3). We did not find official railway data for Paraguay, so there may be an underestimation of this effect for this country. For Brazil, we selected paved, operational, and constructed roads, and railways that were selected by relative surface position and train section for 2021. For Argentina, we consider national and provincial roads paved for the year of 2021. For Paraguay, we only considered the main roads (according to the Atlas nomenclature) for the year 2012, without making a distinction regarding the paving of roads, since this information was not available. The road and railway layers were rasterized using a parameter that creates densified lines, i.e., all cells touched by the line were included as data for rasterization, which implied in more densified lines. This guaranteed that the roads and railways would trim the fragments. After the lines were rasterized, the resulting raster covered 528,983 ha (0.33% from the AF delimitation). We trimmed the fragments of vegetation from the rasterized data generated (Vancine et al. 2024).

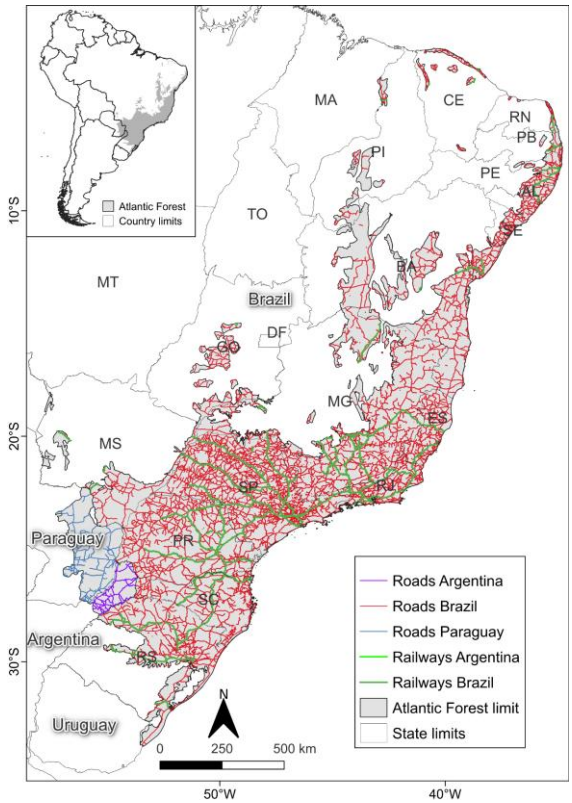


Figure 3. Linear infrastructure (roads and railways) network used to trim the forest vegetation (FV) and native vegetation (NV) fragments within the Atlantic Forest.

Urban areas for Brazil were selected from MapBiomas. For Argentina, this data was downloaded from Instituto Geográfico Nacional (Instituto Geográfico Nacional – IGN, https://www.ign.gob.ar) and for Paraguay from Instituto Nacional de Estadística (Instituto Nacional de Estadística – INE, https://www.ine.gov.py) (Figure 4), and covered 2,401,850 ha (1.48% from the AF limit).

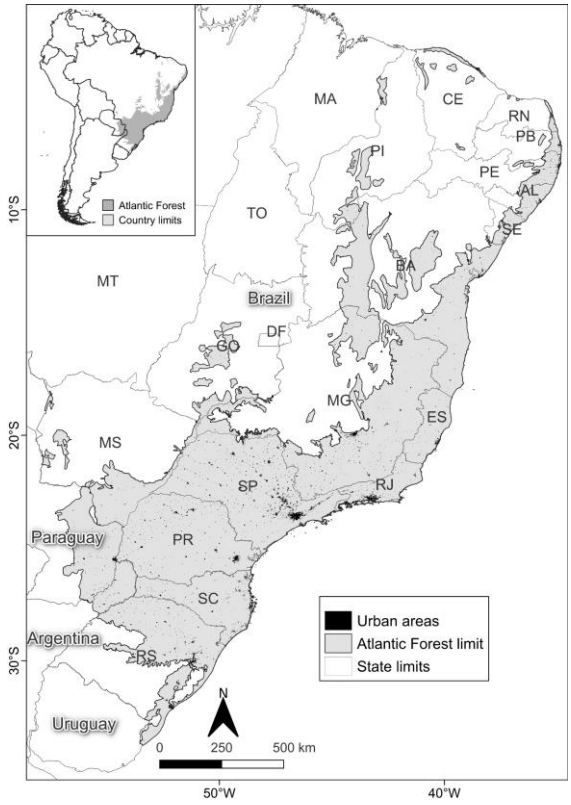


Figure 4. Urban areas within the Atlantic Forest.

Protected areas and indigenous territories

The limits of the protected areas (PA) were downloaded from Protected Planet (UNEP-WCMC and IUCN, 2022, www.protectedplanet.net) for the IUCN categories of protected areas ("Ia", "Ib", "II", "III" and "IV"), which comprises 986 reserves (4,620,245 ha; 2.84% from AF limit) (Figure 5a). These IUCN categories encompass the following protection categories of the Argentina (Municipal Nature Park, National Park, Nature Monument, Private Refuge, Private Wildlife Refuge, Provincial Park, Strict Nature Reserve, Wilderness Nature Reserve and Wildlife Reserve), Brazil (Area of Relevant Ecological Interest, Biological Reserve, Ecological Station, Natural Heritage Private Reserve, Natural Monument, Park, Ramsar Site, Wetland of International Importance, Wildlife Refuge) and Paraguay (National Park, Natural Private Reserve, Natural Reserve, Scientific Monument and

Scientific Reserve). Indigenous territories (IT) for Brazil were downloaded from Fundação Nacional dos Povos Indígenas (Fundação Nacional dos Povos Indígenas, 2020, https://www.gov.br/funai/pt-br) selecting only "Homologated", and for Paraguay from Tierras Indígenas (Tierras Indígenas, 2022, https://www.tierrasindigenas.org), which comprises 1023 territories (1,324,973 ha; 0.81% from AF limit) (Figure 5b).

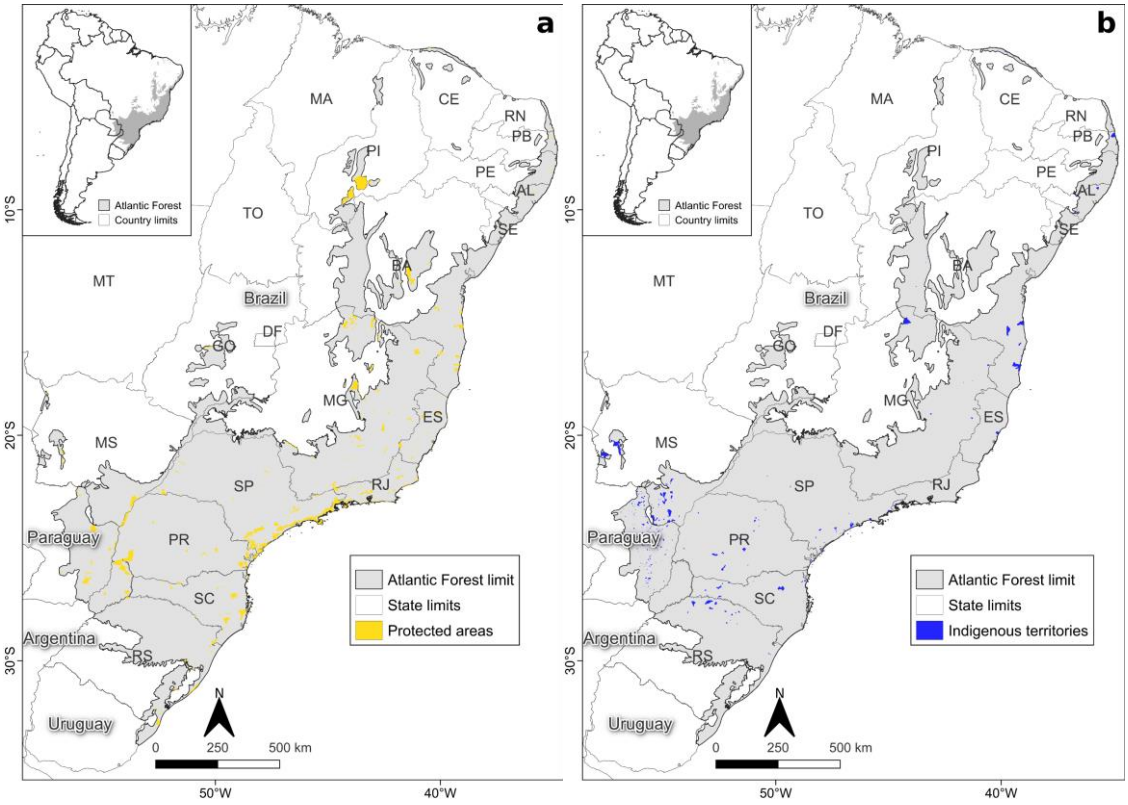


Figure 5. Protected areas (PA) (a) and indigenous territories (IT) (b) within the Atlantic Forest.

Topography data

Topographic metrics were calculated from FABDEM v1.2 (forest and buildings removed Copernicus DEM), an elevation raster map that used machine learning to remove buildings and tree height biases from the Copernicus GLO 30 Digital Elevation Model (DEM) (Hawker et al. 2022) (Figure 6).

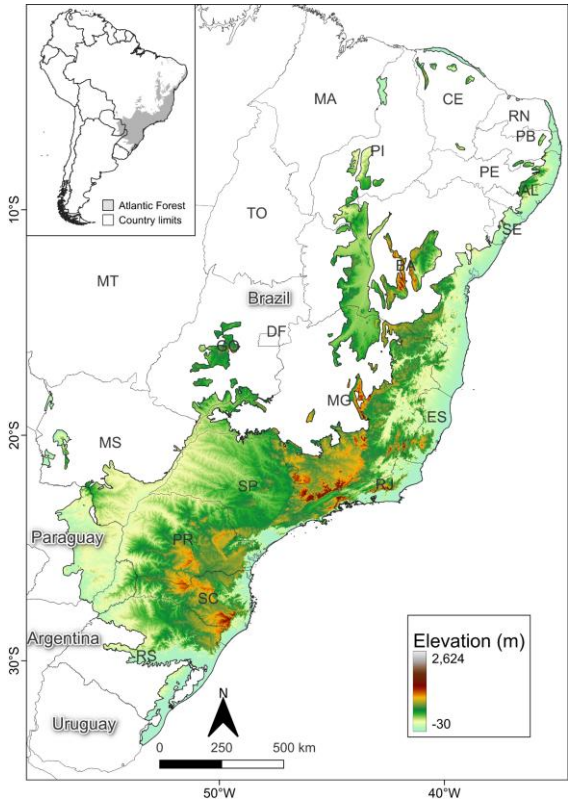


Figure 6. Elevation (meters above sea level) from FABDEM v1.2 across the Atlantic Forest.

Data set source description

Table 2 summarizes all the sources and descriptions of spatial information used to integrate spatial variables presented in the ATLANTIC SPATIAL data set.

Table 2. Source and description of spatial information.

Type of information	Institution	Description
Land Use and Land Cover (LULC)	MapBiomas	Annual LULC information at the 30-m spatial resolution from 1985 to 2021, based on pixel-based random forest classifier of Landsat satellite images using Google Earth Engine. Source: Souza et al. (2020) Site: https://mapbiomas.org

Roads and railways	Instituto Brasileiro de Geografia e Estatística (IBGE) Instituto Geográfico Nacional (IGN) Instituto Nacional de Estadística (INE)	Continuous Cartographic Base of Brazil, 1:250,000. Catalog of Geographical Objects of the Organism and forms part of the Institutional Geospatial Database. Digital Cartography 2012, Directorate General of Statistics, Surveys and Censuses and is merely referential. Sources: Instituto Brasileiro de Geografia e Estatística (IBGE); Instituto Geográfico Nacional (IGN); and Instituto Nacional de Estadística (INE) Sites: https://www.ibge.gov.br; https://www.ign.gob.ar; and https://www.ine.gov.py
Urban areas	MapBiomas Instituto Geográfico Nacional (IGN) Instituto Nacional de Estadística (INE)	Annual LULC information at the 30-m spatial resolution from 1985 to 2021, based on pixel-based random forest classifier of Landsat satellite images using Google Earth Engine. Catalog of Geographical Objects of the Organism and forms part of the Institutional Geospatial Database. Digital Cartography 2012, Directorate General of Statistics, Surveys and Censuses and is merely referential. Sources: Souza et al. (2020), Instituto Geográfico Nacional (IGN) and Instituto Nacional de Estadística (INE) Sites: https://mapbiomas.org, https://www.ign.gob.ar and https://www.ine.gov.py
Protected areas	Protected Planet	Up-to-date and complete source of data on protected areas and other effective area-based conservation measures, updated monthly with submissions from governments, non-governmental organizations, landowners and communities. Source: Protected Planet Site: www.protectedplanet.net
Indigenous territories	Fundação Nacional dos Povos Indígenas (FUNAI) Tierras Indígenas	Official indigenist body of the Brazilian State, which promotes studies of identification, delimitation, demarcation, land regularization and registration of

		lands occupied by indigenous peoples, in addition to monitoring and inspecting indigenous lands. Interactive online platform that provides accurate maps and critical information on the lands and territories of indigenous peoples and communities in Paraguay. Sources: FUNAI and Tierras Indígenas Sites: https://www.gov.br/funai/pt-br and https://www.tierrasindigenas.org
Topography	Forest and Buildings Removed Copernicus DEM (FABDEM) v1.2	Elevation raster map that used machine learning to remove building and tree height biases from the Copernicus GLO 30 Digital Elevation Model (DEM) Source: Hawker et al. (2022) Site: https://www.fathom.global/product/fabdem

Landscape metrics

We calculated 39 landscape metrics of nine types (Table 3) based on the habitat map (binary habitat/non-habitat map, Figure 2c) of FV and NV and multi-class map (31 classes, Figure 2a). The values of the landscape metrics were spatialized to the cells. The metrics derived from FV and NV were based on data trimmed by linear structure (roads and railways). Here, to exemplify the method used for calculating of landscape metrics, we display two toy landscapes (Fletcher and Fortin 2018): a binary raster and a multi-class raster (Figure 7).

Toy landscapes (Figure 7): two raster layers (16×16 cells with spatial resolution of 100 m). Cells of the toy landscape (binary) were filled with 0 and 1 values, where 0 represents not-habitat and 1 represents habitat. For the toy landscape (multi-class), cells were filled with values from 0 to 5, where each value represents a different LULC class.

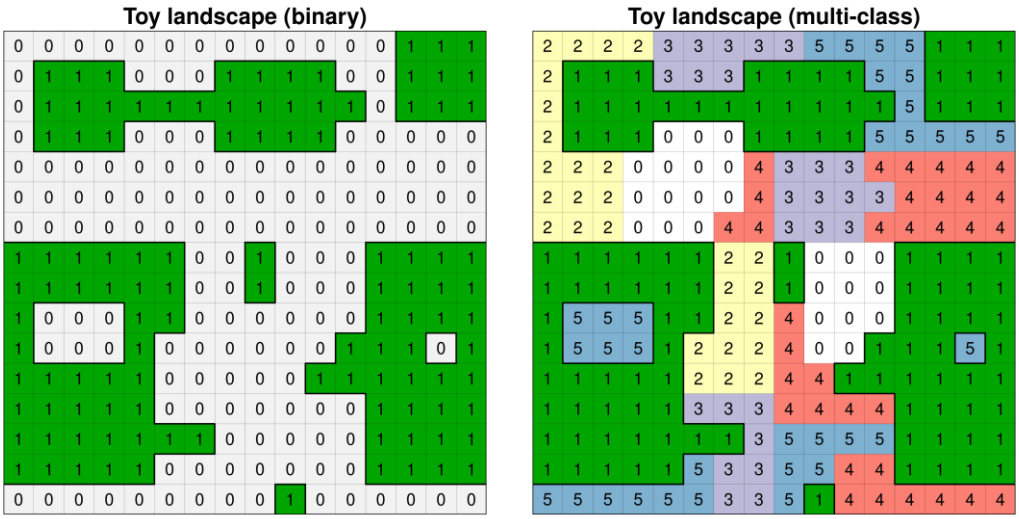


Figure 7. Toy landscapes. Toy landscape (binary, on the left) has 0 and 1 values (non-habitat/habitat), and toy landscape (multi-class, on the right) has values from 0 to 5 (land cover classes). Each cell has 100 m of resolution.

Table 3. Landscape metrics used and their description. Edge depth is the minimum distance at which cells are classified as edges, those that are further away are classified as cores. Gap-crossing considers the ability of an organism to cross non-habitat gaps, characterizing the distance to functional connectivity. Scale is the radius of the buffer to which the moving window is rotated to impute the effect of different scales on landscape metrics.

Metric	Metric type	Short description	Values	Edge depth (in meters)	Gap-crossing (in meters)	Scale (buffer radius in meters)	Reference
1. Fragment ID	Fragment	Fragment identification (cells clumped in its vicinity, considering the 8 neighboring cells)	Units	None	None	None	McGarigal et al. (2023)
2. Fragment area	Fragment	Fragment area (sum of the area of all cells belonging to each fragment ID)	Hectares	None	None	None	McGarigal et al. (2023)
3. Percentage of fragments	Fragment	Percentage of fragments in the vicinity (average neighborhood values for different buffer sizes)	0 to 100	None	None	50, 100, 150, 200, 250, 500, 750, 1000, 1500, 2000, 2500, 5000, 7500, 10000	McGarigal et al. (2023)
4. Patch ID	Patch	Patch identification (cells clumped in its vicinity, considering the 8 neighboring cells), discarding branches and corridors	Units	30	None	None	McGarigal et al. (2023)
5. Patch area	Patch	Patch area (sum of the area of all cells belonging to each patch ID), discarding branches and corridors	Hectares	30	None	None	McGarigal et al. (2023)
6. Patch area original	Patch	Patch area assigned to the original fragment. Here each cell of a fragment will be assigned the value of the sum of the areas of all patches contained in the fragment	Hectares	30	None	None	McGarigal et al. (2023)
7. Number of	Patch	Number of patches (number of patch ID	Units	30	None	None	McGarigal et

Metric	Metric type	Short description	Values	Edge depth (in meters)	Gap-crossing (in meters)	Scale (buffer radius in meters)	Reference
patches		within a fragment) assigned to the original fragment. Here each cell of a fragment will be assigned the value number of patches contained in the fragment					al. (2023)
8. Morphology	Morphology	Identifies landscape morphologies: matrix (0), core (1), edge (2), corridor (3), stepping stone (4), branch (5) and perforation (6)	0 to 6	30	None	None	Soille and Vogt (2009)
9. Matrix	Morphology	Identify matrix (non-habitat cells = 1)	0 and 1	30	None	None	Soille and Vogt (2009)
10. Core	Morphology	Identify fragment cores (core cells = 1)	0 and 1	30	None	None	Soille and Vogt (2009)
11. Edge	Morphology	Identify fragment edges (external edge cells = 1)	0 and 1	30	None	None	Soille and Vogt (2009)
12. Corridor	Morphology	Identify corridors (linear elements that connect core cells = 1)	0 and 1	30	None	None	Soille and Vogt (2009)
13. Branch	Morphology	Identify branches (linear elements that do not connect core cells = 1)	0 and 1	30	None	None	Soille and Vogt (2009)
14. Stepping stone	Morphology	Identify stepping stones (isolated small elements without core cells = 1)	0 and 1	30	None	None	Soille and Vogt (2009)
15. Perforation	Morphology	Identify perforations (edge that compose the internal edge of a fragment = 1)	0 and 1	30	None	None	Soille and Vogt (2009)
16. Core	Core and edge	Identify core cells (core = 1)	0 and 1	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
17. Core ID	Core and	Core identification (core cells clumped in	Units	30, 60, 90,	None	None	McGarigal et

Metric	Metric type	Short description	Values	Edge depth (in meters)	Gap-crossing (in meters)	Scale (buffer radius in meters)	Reference
	edge	its vicinity, considering the 8 neighboring cells)		120, 240			al. (2023)
18. Core area	Core and edge	Core area (sum of the area of all core cells belonging to that core ID)	Hectares	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
19. Core area original	Core and edge	Core area assigned to the original fragment. Here each cell of a fragment will be assigned the value total area of all cores contained in the fragment	Hectares	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
20. Number of cores	Core and edge	Number of cores within a fragment. Here each cell of a fragment will be assigned the value number of cores contained in the fragment	Units	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
21. Edge	Core and edge	Identify edge cells (edge = 1). This includes both external and internal edges (perforations)	0 and 1	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
22. Edge ID	Core and edge	Edge identification (cells clumped in its vicinity, considering the 8 neighboring cells)	Units	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
23. Edge area	Core and edge	Edge area (sum of the area of all edge cells belonging to that edge ID)	Hectares	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
24. Edge area original	Core and edge	Edge area assigned to the original fragment. Here each cell of a fragment will be assigned the value total area edge in the fragment	Hectares	30, 60, 90, 120, 240	None	None	McGarigal et al. (2023)
25. Percentage of core	Core and edge	Percentage of core cells within the vicinity (average neighborhood values for different buffer sizes)	0 to 100	30, 60, 90, 120, 240	None	50, 100, 150, 200, 250, 500, 750, 1000, 1500, 2000, 2500	McGarigal et al. (2023)

Metric	Metric type	Short description	Values	Edge depth (in meters)	Gap-crossing (in meters)	Scale (buffer radius in meters)	Reference
26. Percentage of edges	Core and edge	Percentage of edge cells in the vicinity (average neighborhood values for different buffer sizes)	0 to 100	30, 60, 90, 120, 240	None	50, 100, 150, 200, 250, 500, 750, 1000, 1500, 2000, 2500	McGarigal et al. (2023)
27. Perimeter	Perimeter	Perimeter (number of cells sides of a fragment facing the matrix, including any internal holes)	Meters	30	None	None	McGarigal et al. (2023)
28. Perimeter-area ratio	Perimeter	Perimeter-area ratio (ratio between fragment perimeter and fragment area)	0 to infinity	30	None	None	McGarigal et al. (2023)
29. Distance inside	Distance	Euclidean distance to the nearest fragment edge cell, inside the fragment	Meters	None	None	None	Ribeiro et al. (2009)
30. Distance outside	Distance	Euclidean distance to the nearest fragment edge cell, outside the fragment	Meters	None	None	None	Ribeiro et al. (2009)
31. Distance	Distance	Euclidean distance to the nearest fragment edge cell, both inside (negative) and outside (positive) the fragment	Meters	None	None	None	Ribeiro et al. (2009)
32. Structural connectivity	Structural connectivity	Structural connectivity (represents the area of habitat structurally connected to a patch, taking into account corridors, branches and possibly other patches, but disregarding the area of the own patch)	Hectares	30	None	None	Ribeiro et al. (2009)
33. Structurally connected area	Structural connectivity	Structurally connected area (calculated from the original fragment, where the structural connectivity of the patches was associated with the fragment)	Hectares	30	None	None	Ribeiro et al. (2009)
34. Functionally connected dilation	Functional connectivity	Functionally connected dilation (fragments dilate by half the value of the organism's gap-crossing capacity)	Hectares	None	60, 120, 180, 240, 300, 600	None	Ribeiro et al. (2009)

Metric	Metric type	Short description	Values	Edge depth (in meters)	Gap-crossing (in meters)	Scale (buffer radius in meters)	Reference
35. Functionally connected ID	Functional connectivity	Functionally connected identification (fragments that are at the shortest distance from the gap-crossing are grouped, receiving the same ID)	Hectares	None	60, 120, 180, 240, 300, 600	None	Ribeiro et al. (2009)
36. Functionally connected area	Functional connectivity	Functionally connected area (area of these fragments with the same ID was summed)	Hectares	None	60, 120, 180, 240, 300, 600	None	Ribeiro et al. (2009)
37. Functional connectivity	Functional connectivity	Functional connectivity (difference between the functionally connected area and the fragment size)	Hectares	None	60, 120, 180, 240, 300, 600	None	Ribeiro et al. (2009)
38. Landscape Shannon diversity	Landscape diversity	Landscape Shannon diversity (consider the number of classes in each class cell within the window of analysis for Shannon index)	0 to infinity	None	None	50, 100, 150, 200, 250, 500, 750, 1000, 1500, 2000	Rocchini et al. (2013)
39. Landscape Simpson diversity	Landscape diversity	Landscape Simpson diversity (consider the number of classes in each class cell within the window of analysis for Shannon index)	0 to 1	None	None	50, 100, 150, 200, 250, 500, 750, 1000, 1500, 2000	Rocchini et al. (2013)

Fragment area metrics (Figure 8): considering a binary habitat map, all cells of habitat were clumped with other cells of habitat in its vicinity (considering the 8 neighboring cells). Each clump of habitat was called a fragment and was given an ID (**Metric 1: Fragment ID**). For each fragment ID, its area (**Metric 2: Fragment area**) was calculated as the sum of the area of all cells belonging to that fragment ID. The unit used to calculate the area is hectares. Non-habitat cells are returned as NULL values.

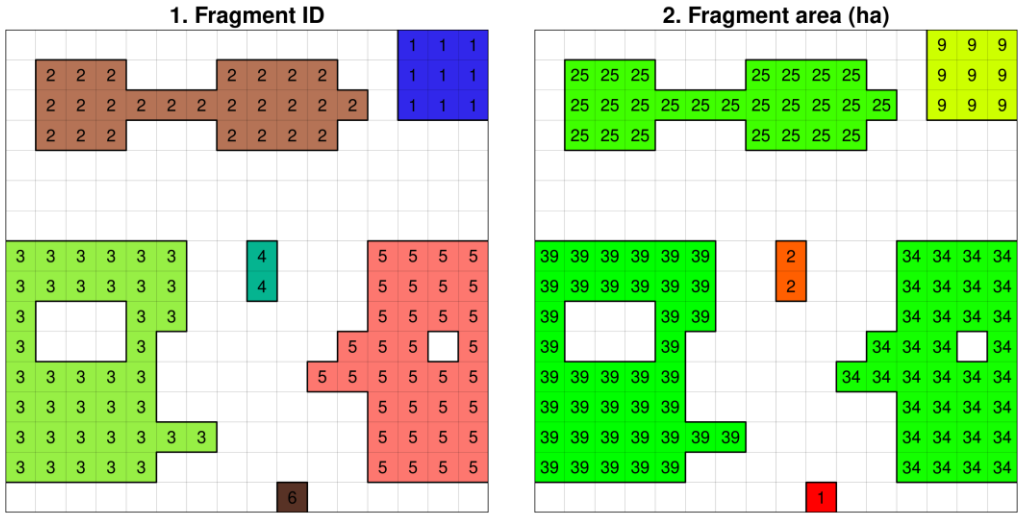


Figure 8. Fragment area metrics. Metric 1: Fragment ID is the fragment identification. Metric 2: Fragment area (ha) is the fragment area calculated in hectares. Each cell has 100 m of side length in the toy landscape.

Percentage of fragments metric (Figure 9): considering a binary habitat map, each cell of the map presented a value of the percentage of fragments within a circular window with a given size, centered in the focal cell (amount of habitat cells/total number of cells in the window). It varies between 0% and 100% (**Metric 3: Percentage of fragments**). Buffer radius represented half the size of a circular window, e.g., for a buffer size of 50 m, the window size was 100 m. Buffer radii used: 50 m, 100 m, 150 m, 200 m, 250 m, 500 m, 750 m, 1,000 m, 1,500 m, 2,000 m, 2,500 m, 5,000 m, 7,500 m, 10,000 m.

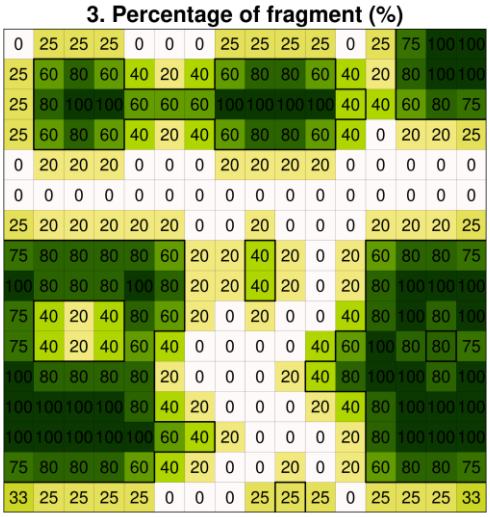


Figure 9. Percentage of fragments metric. Metric 3: fragment percentage for a buffer radius of 100 m (i.e., a circular window with 200 m size), as illustration in the toy landscape.

Patch area metrics (Figure 10): considering a binary habitat map, these metrics are equivalent to the fragment area metric, but discards habitat branches and corridors that are closer than a given edge depth from the edge between the fragment and the matrix. The result is a map of clusters (considering the 8 neighboring cells) of cells, which does not consider corridors or branches. Each habitat cluster was called a patch and given an ID (**Metric 4: Patch ID**). For each patch ID, its area (**Metric 5: Patch area**) was calculated as the sum of the area of all cells belonging to that patch ID. The patch area has also been attributed to the original fragment ID, which sums the area of all patches belonging to the same fragment (**Metric 6: Patch area original**). The amount of different patch IDs for a fragment is also calculated (**Metric 7: Number of patches**). Edge depths considered: 30 m. The unit used to calculate the area was hectares. Non-habitat cells were assigned with NULL values.

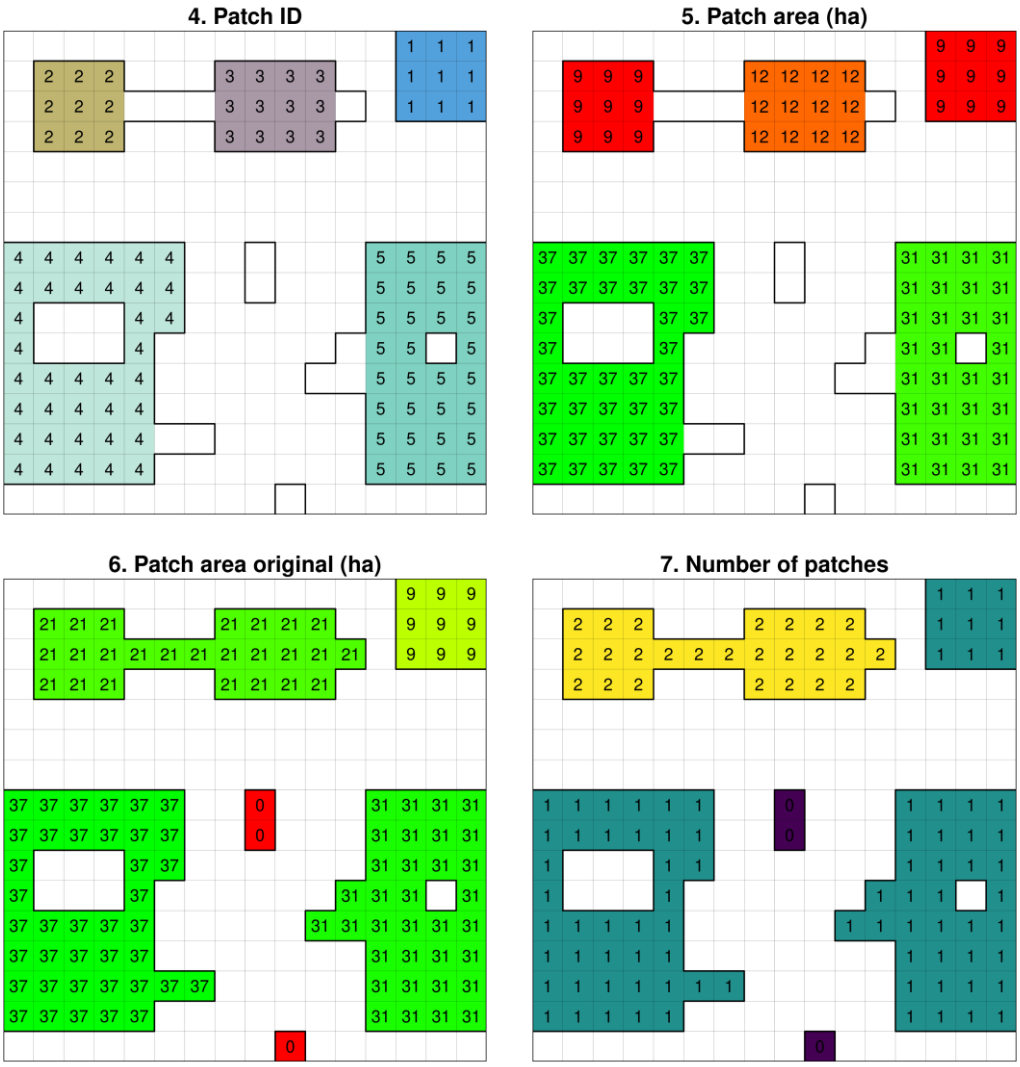
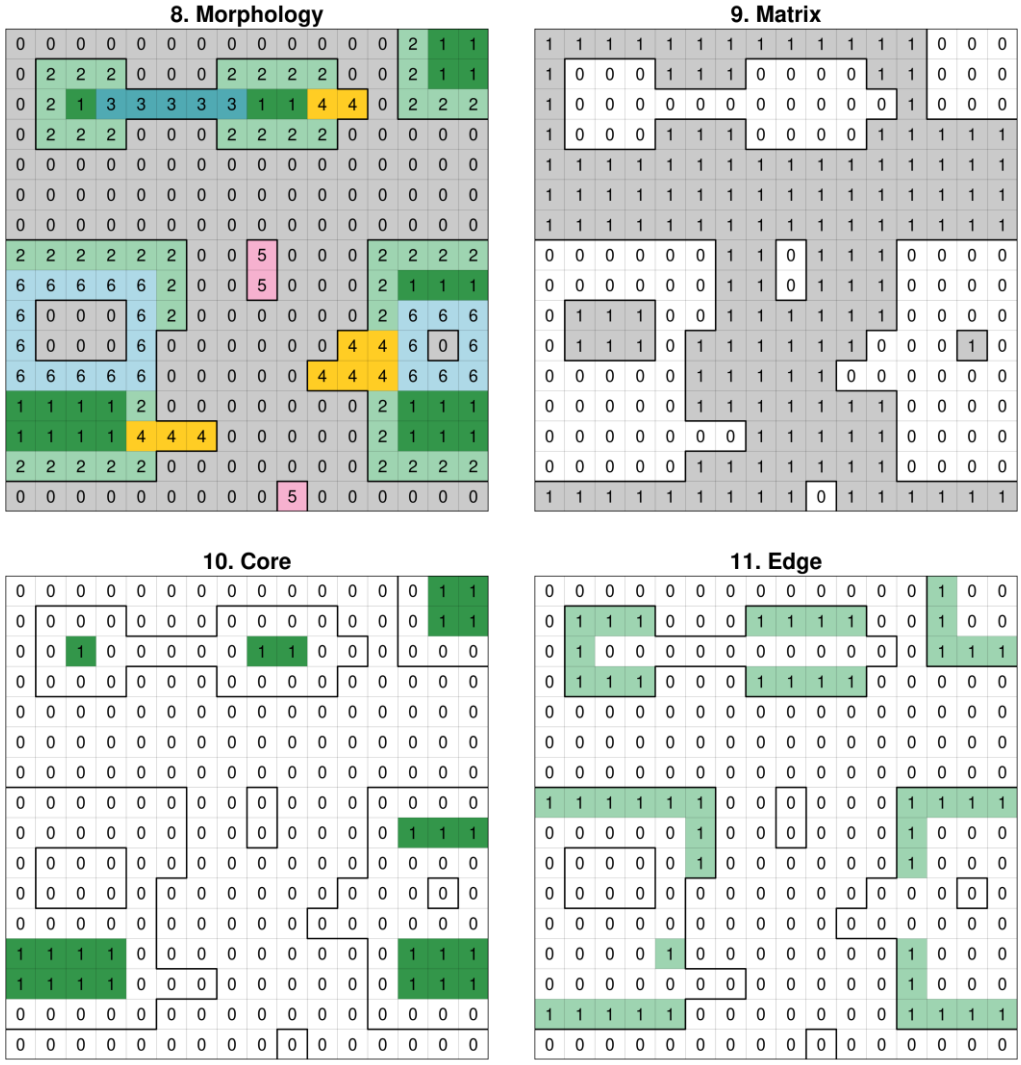


Figure 10. Patch area metrics. Metric 4: Patch ID is the patch identification. Metric 5: Patch area (ha) is the patch area in hectares. Metric 6: Patch area original (ha) is the patch area for the original fragment in hectares. Metric 7: Number of patches is the number of patches for the original fragment. The edge depth was chosen as 50 m in this illustrative example in the toy landscape.

4. Morphological metrics (Figure 11): considering a binary habitat map, these metrics classify the landscape as a set of morphological/structural categories (**Metric 8: Morphology**), i.e., whether a cell is matrix, core, edge, corridor, branch, stepping stone or perforation. This classification is made by considering an edge depth to distinguish what if the edge and the core of a habitat fragment. Matrices are the non-habitat cells from the binary map (**Metric 9: Matrix**). Cores are habitat cells after removing the edge cells (**Metric 10: Core**). Edges are habitat cells that are closer to the edge than the chosen edge depth, but are not corridor, branch, stepping stone or perforation (**Metric 11: Edge**). Corridors are edge

cells that connect two or more core cells (**Metric 12: Corridor**). Branches are edge cells that do not connect cores (**Metric 13: Branch**). Stepping stones are edge cells that do not have core cells inside them (**Metric 14: Stepping stone**). Perforations are edge cells that compose the internal edge of a fragment (**Metric 15: Perforation**). Edge depths considered: 30 m.



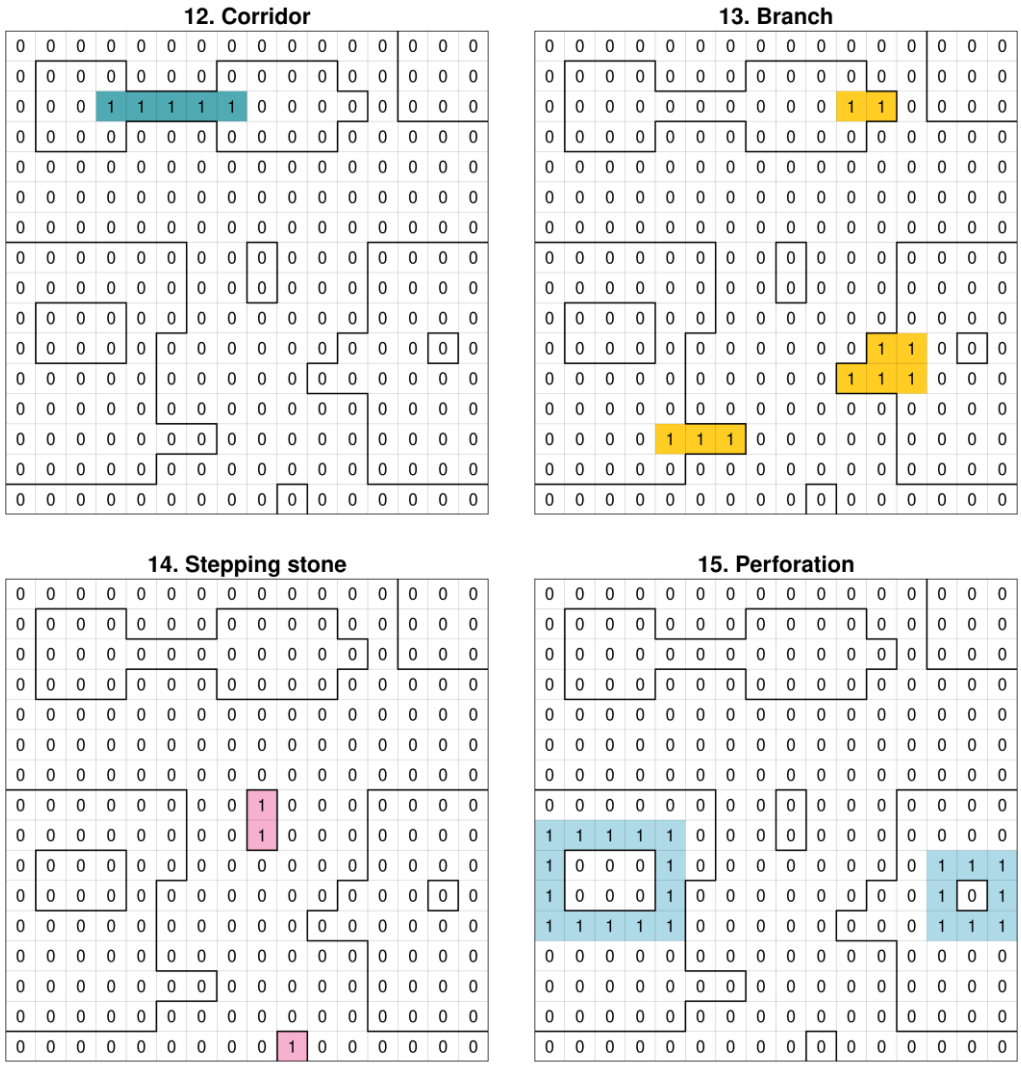
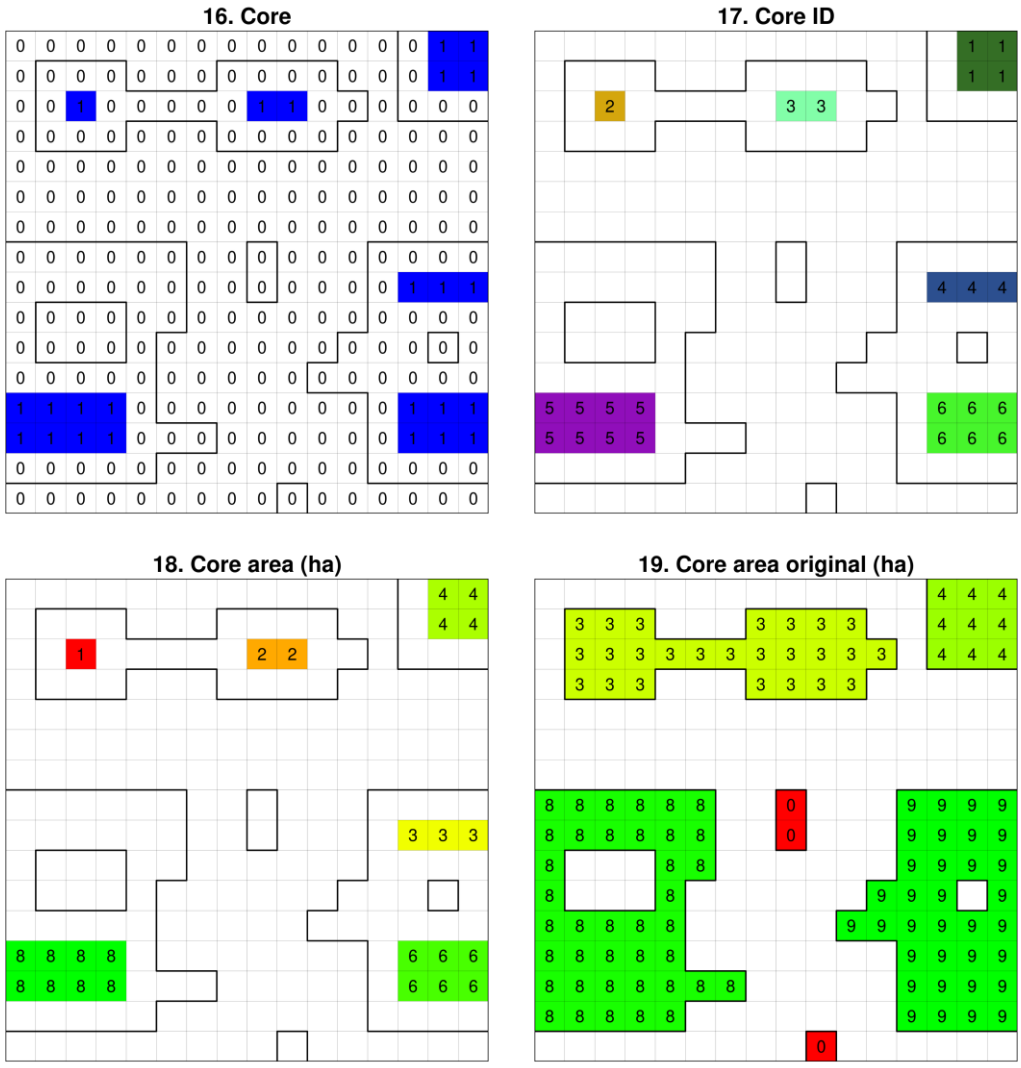


Figure 11. Morphological metrics. Metric 8: Landscape morphologies: matrix (0), core (1), edge (2), corridor (3), stepping stone (4), branch (5) and perforation (6). Metric 9: matrix = non-habitat cells. Metric 10: Core = habitat cells, removing the edge cells. Metric 11: Edge =habitat cells which are closer to the habitat edge than the chosen edge depth. Metric 12: Corridor = edge cells that connect two or more core cells. Metric 13: Branch = edge cells that do not connect cores. Metric 14: Stepping stone = edge cells that do not have core cells. Metric 15: Perforation = edge cells that compose the internal edge of a fragment. The edge depth used in this illustrative figure was 50 m.

Core and edge area metrics (Figure 12): considering a binary habitat map, these metrics classify cells in core or edge, considering a depth of edge. Cells that are closer (or at the same distance) from the edge than the edge depth are classified as edges, those that are further away inside the habitat patches are classified as core. We clumped the core and edge cells (considering the 8 neighboring cells; **Metric 16: Core** and **Metric 21: Edge**) and gave

it an ID (**Metric 17: Core ID** and **Metric 22: Edge ID**). For each core and edge ID, its area was calculated as the sum of the area of all cells belonging to that core or edge ID (**Metric 18: Core area** and **Metric 23: Edge area**). We also calculated the area of a core or edge of the original fragment by summing the area of the core or edge cells belonging to a fragment (**Metric 19: Core area original** and **Metric 24: Edge area original**), and the number of cores (**Metric 20: Number of cores**), which was the number of different cores IDs for a fragment. Notice that the Metric 21 (Edge) differs from morphological classification of edges (Metric 11), because the latter subdivides edges cells into edges, corridors, branches, stepping stones and perforations. Metric 21 includes all these in a single category. Edge depths considered: 30 m, 60 m, 120 m, 240 m. The unit used to calculate the area was hectares. Non-habitat cells were assigned with NULL values, except for core and edge binary maps.



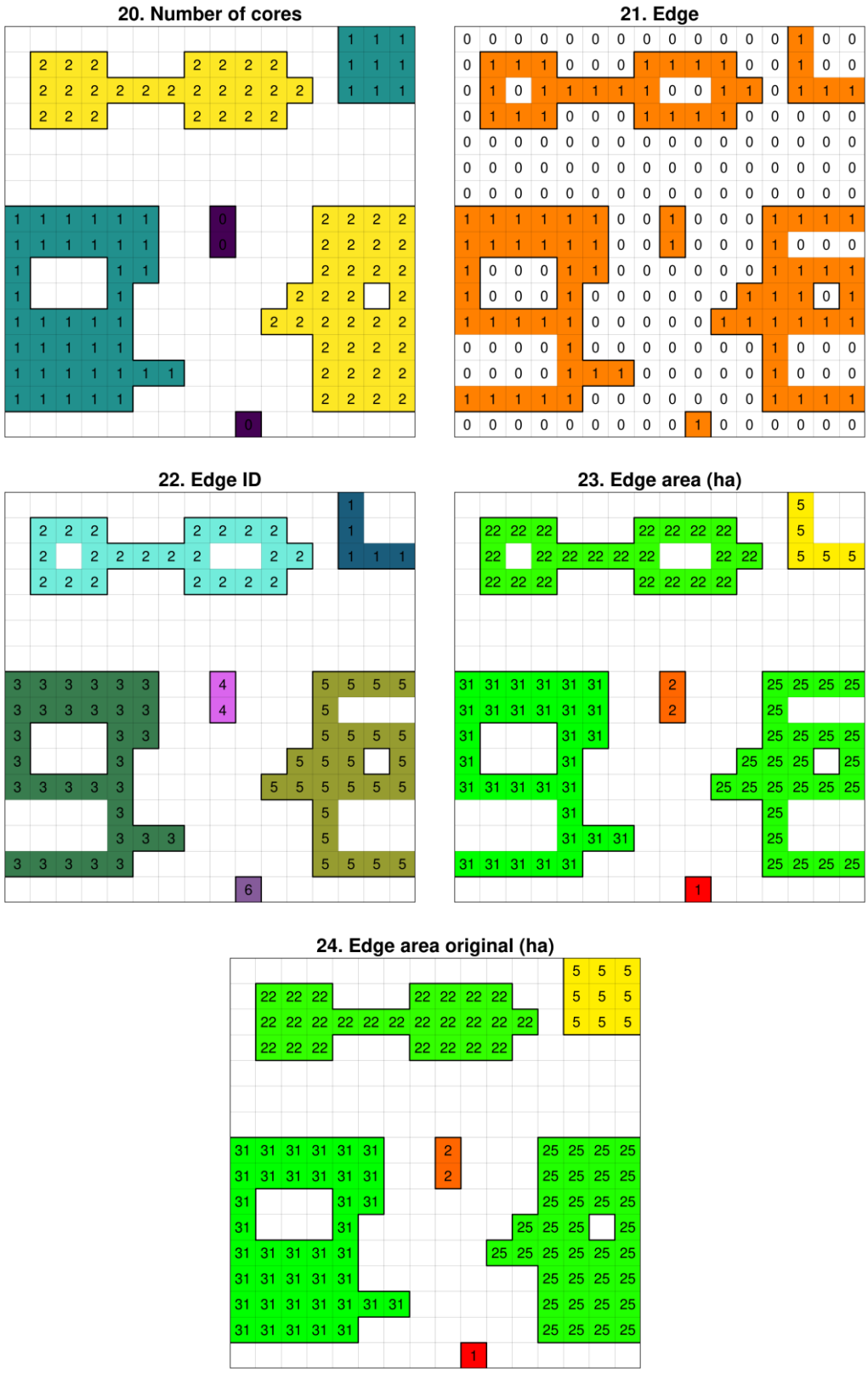


Figure 12. Edge and core area metrics. Metric 16: Core is the binary core and not-core. Metric 17: Core ID is the core identification. Metric 18: Core area (ha) is the core area in hectares. Metric 19: Core area original (ha) is the core area for the original fragment in hectares. Metric 20: Number of cores is the number of cores for the original fragment.

Metric 21: Edge is the binary edge and not-edge. Metric 22: Edge ID is the edge identification. Metric 23: Edge area (ha) is the edge area in hectares. Metric 24: Edge area original (ha) is the edge area for the original fragment in hectares. Each cell of the toy landscape has 100 m of side length and the edge depth was chosen as 50 m in this illustrative example.

Percentage of core and edge metrics (Figure 13): considering a binary habitat map, each cell of the map presents a value of the proportion of core or edge area within a circle window with a given size, centered in the focal cell (amount of core or edge cells/total number of cells in the window). It varies between 0 and 100% (**Metric 25: Percentage of core** and **Metric 26: Percentage of edges**). Edge depths considered: 30 m, 60 m, 120 m, 240 m. Buffer radius represented half the size of a circular window, e.g., for a buffer size of 50 m, the window size was 100 m. Buffer radius used: 50 m, 100 m, 150 m, 200 m, 250 m, 500 m, 750 m, 1000 m, 1500 m, 2000 m, 2500 m.

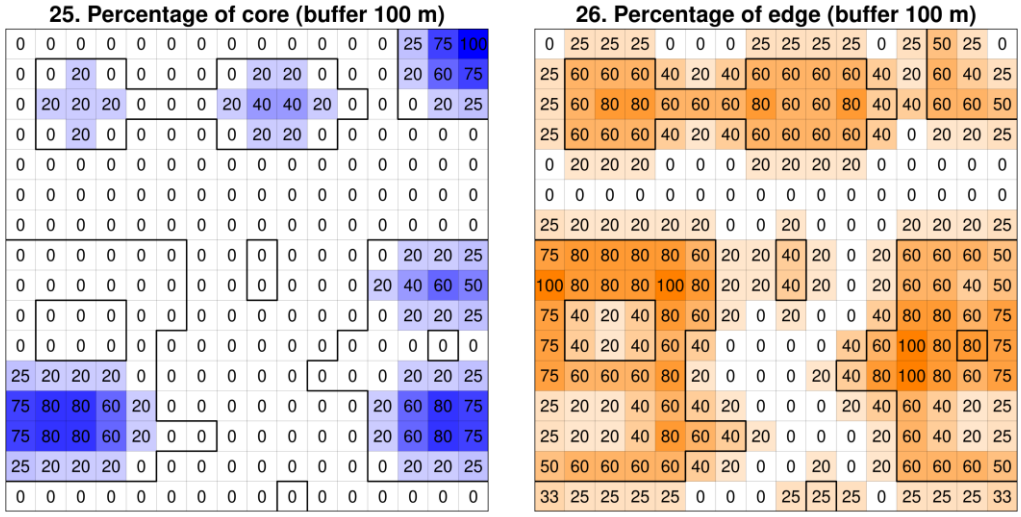


Figure 13. Percentage of core and edge metrics. Metric 25: Percentage of core and Metric 26: Percentage of edge for a circular window with 100 m size, as an illustrative example in the toy landscape.

Perimeter metrics (Figure 14): considering a binary habitat map, the perimeter is the number of cells sides of a fragment facing the matrix, including any internal holes, in meters (**Metric 27: Perimeter**). Perimeter-area ratio is the ratio between fragment perimeter and fragment area, without a measurement unit (**Metric 28: Perimeter-area ratio**). This is a simple measure of shape complexity, the higher its value, the greater the complexity of the

fragment shape. A limitation in using this metric as a shape complexity index is that it varies with the area of the fragment. For example, holding shape constant, an increase in fragment area will cause a decrease in the perimeter-area ratio. Edge depths considered: 30 m. Non-habitat cells were assigned with NULL values.

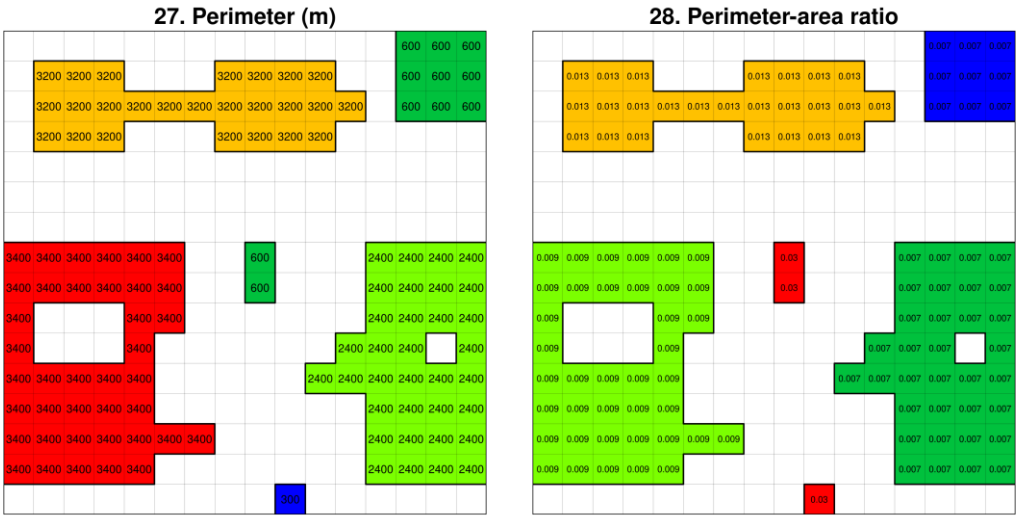


Figure 14. Perimeter metrics. Metric 27: Perimeter (m) is the number of pixel sides of a fragment facing the matrix. Metric 28: Perimeter-area ratio is a shape complexity metric.

Distance metrics (Figure 15): considering a binary habitat map, these metrics are based on maps of Euclidean distance inside and outside from habitat edges, in meters. Each cell outside habitat (matrix, non-habitat) was given a positive value equal to the distance to the nearest habitat cell edge (**Metric 29: Distance outside**). Cells inside habitat were given a negative value, corresponding to the distance to the nearest edge with matrix cells (**Metric 30: Distance inside**). Inside and outside distances were combined in a metric by summing outside and inside distance metrics, only for FV and NV (**Metric 31: Distance**).

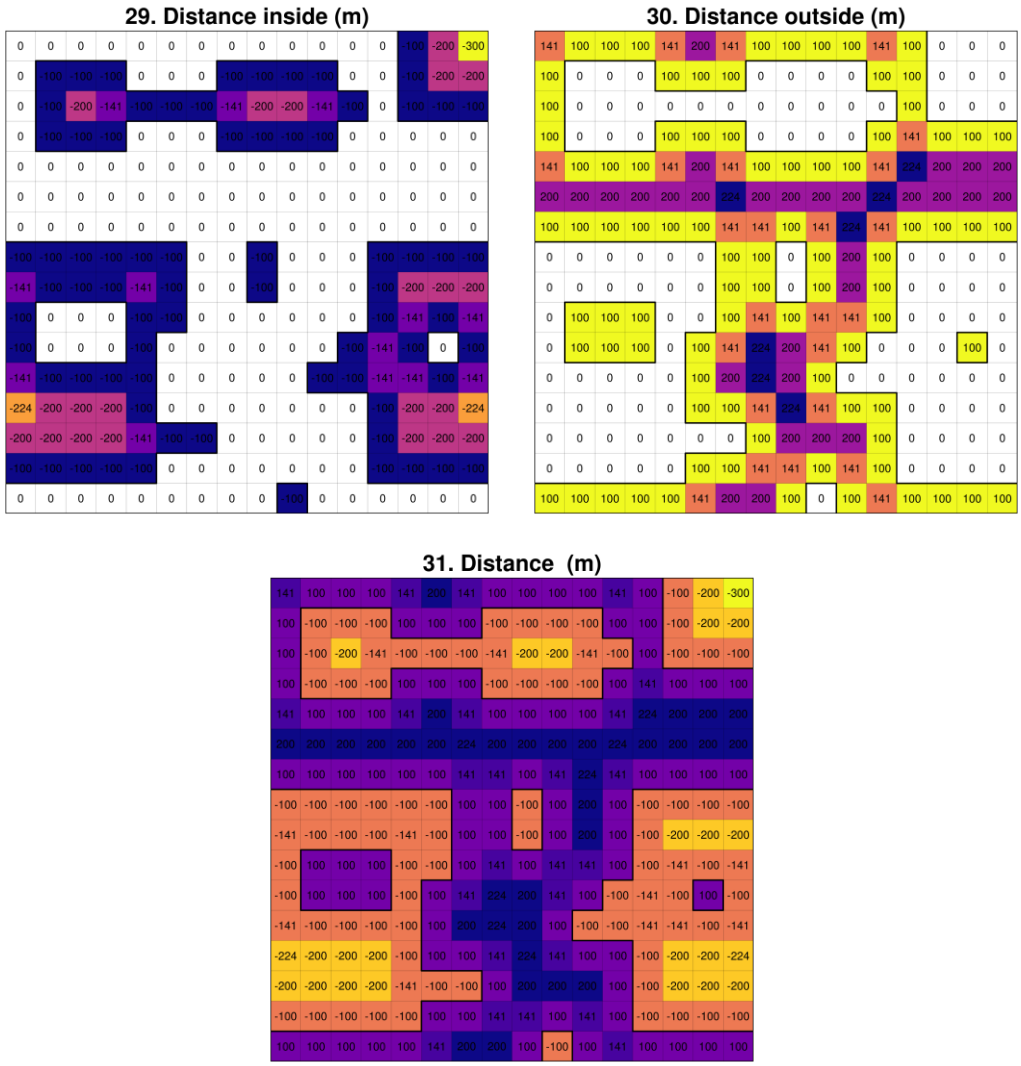


Figure 15. Distance metrics. Metric 29: Distance inside (m) is the distance inside from habitat with negative values. Metric 30: Distance outside (m) is the outside distance from habitat with positive values. Metric 31: Distance (m) is the distance to habitat (FV and NV only) resulting from summing Distance inside (m) and Distance outside (m).

Structural connectivity metrics (Figure 16): considering a binary habitat map, these metrics represent the area of habitat structurally connected to a patch, considering corridors, branches, and possibly other patches (if the corridor connects these patches). In practice, it is calculated as the difference between the fragment area and the patch area. When a patch has no corridors or branches, its structural connectivity equals zero (i.e., it is not structurally connected to any other habitat). Each patch cell is assigned a structural connectivity value (**Metric 32: Structural connectivity**). The structural connected area was calculated from the original fragment, where the structural connectivity of the patches was associated with

the fragment (**Metric 33: Connected structural area**). The definition of structural connectivity depends on what is considered patch, corridor, and branch, so this metric depends on the edge depth value considered. For the AF the depth of the chosen edge was 30 m. The unit used to calculate the area was hectares. Non-habitat cells were assigned with NULL values.

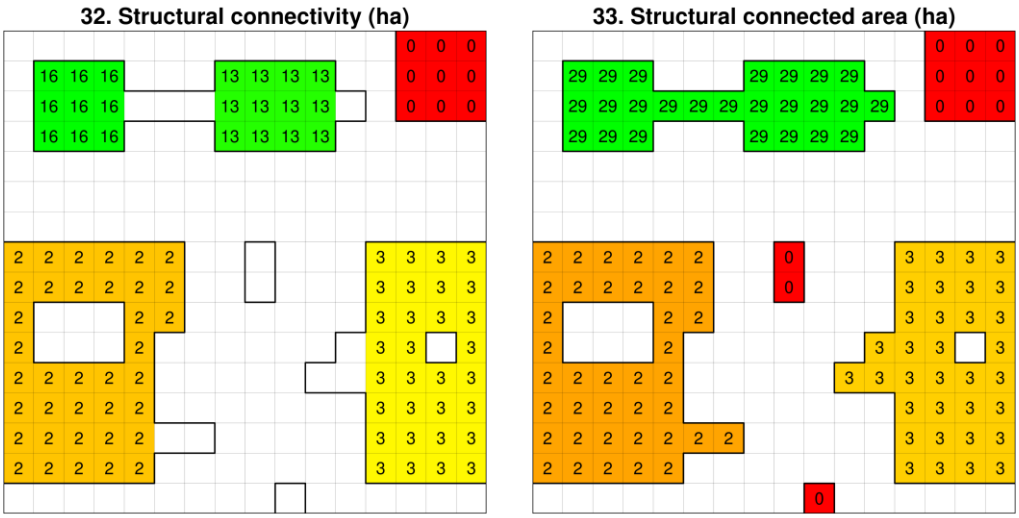


Figure 16. Structural connectivity metrics. Metric 32: Structural connectivity (ha) is the area of habitat structurally connected to a patch only for patches in hectares. Metric 33: Structural connected area (ha) is the area of structurally connected habitat to fragments in hectares.

Functional connectivity metrics (Figure 17): considering a binary habitat map, these metrics represent the habitat area functionally linked to a fragment, considering the ability of an organism to cross non-habitat gaps (gap-crossing value). First, the fragments are expanded/dilated by half the value of the organism's gap-crossing capacity (e.g., if an organism crosses 200 m, the fragments will be dilated by 100 m along their entire perimeter) (**Metric 34: Functionally connected dilation**). Then, the fragments that are at the shortest distance from the gap-crossing are grouped, receiving the same ID (**Metric 35: Functionally connected ID**). Then, the area of these fragments with the same ID was summed (**Metric 36: Functionally connected area**). Finally, to obtain the functional connectivity, the difference between the functionally connected area and the fragment area was calculated, representing how much habitat is accessible from a habitat fragment for an organism with a given gap-crossing ability, excluding the area of the very same fragment (**Metric 37: Functional connectivity**). Crossing capacities considered for the AF: 60 m, 120 m, 180 m,

240 m, 300 m, 600 m. The unit used to calculate the area was hectares. Non-habitat cells were assigned with NULL values.

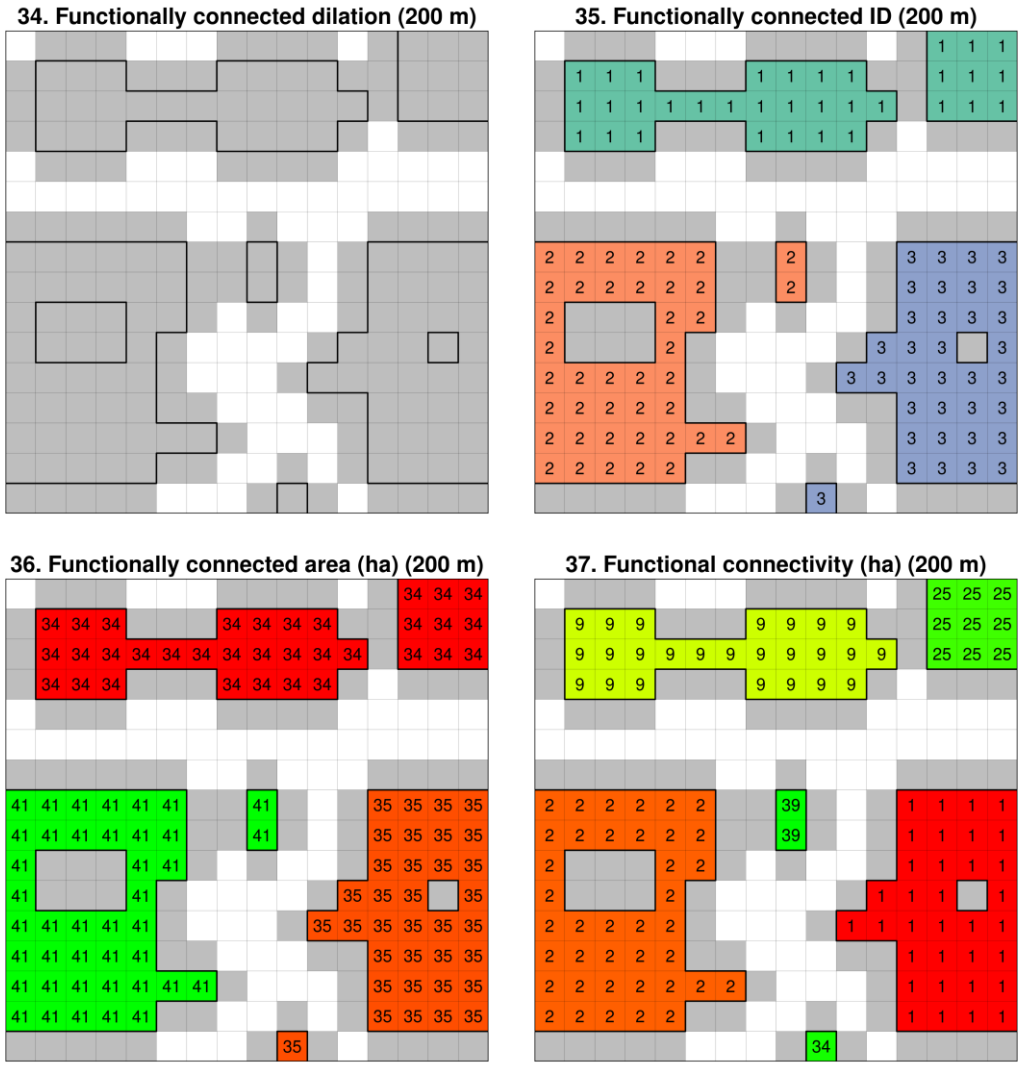


Figure 17. Functional connectivity metrics. Metric 34: Functionally connected dilation (200 m) is the dilation of fragments for gap-crossing of 100 m (gray pixels). Metric 35: Functionally connected ID (200 m) is the functionally connected area identification. Metric 36: Functionally connected area (ha) is the fragment area connected in hectares. Metric 37: Functional connectivity (ha) (200 m) is the functional connectivity in hectares.

Landscape diversity metrics (Figure 18): considering a multi-class map, each cell of the map presented a value of the diversity of LULC classes within a square window with a given size, centered in the focal cell. Diversity (Shannon and Simpson) indices consider the number of classes in each class cell within the window of analysis. Shannon's diversity values are positive values and vary between 0 and infinity (**Metric 38: Landscape diversity**

(Shannon)) and Simpson's diversity values vary between 0 and 1 (**Metric 39: Landscape diversity (Simpson)**). Buffer radius represented half the size of a square window, e.g., for a buffer size of 50 m, the window size was 100 m. Buffer radii used: 50 m, 100 m, 150 m, 200 m, 250 m, 500 m, 750 m, 1000 m, 1500 m and 2000 m. Due to computational limitations, we were unable to calculate landscape diversity metrics for the 2,500 m buffer radius.

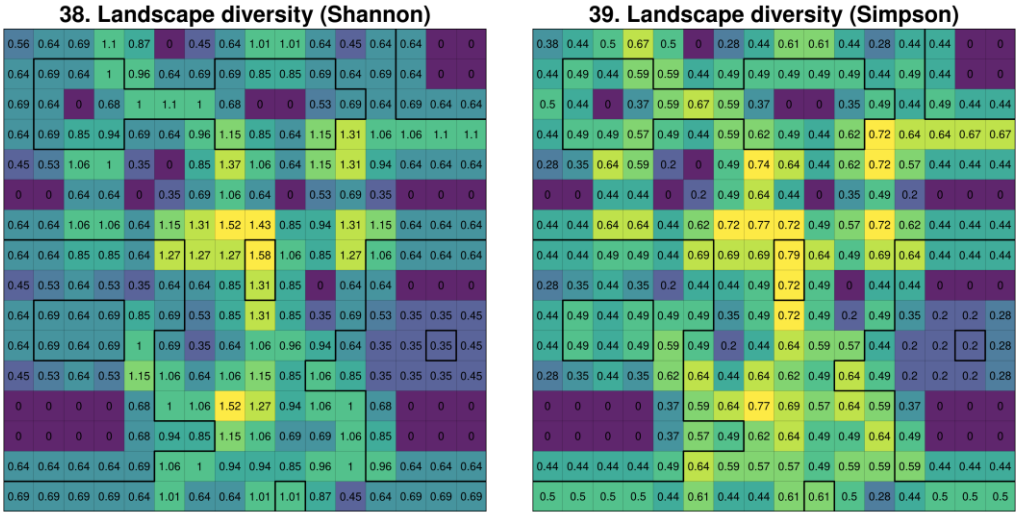


Figure 18. Landscape diversity metrics. Metric 38: Landscape diversity (Shannon) and Metric 39: Landscape diversity (Simpson) indices for a square window with 100 m size, in the illustrative example for the toy landscape.

Topographic metrics

We calculated six metrics of topography using a Digital Elevation Model (DEM) map from FABDEM v1.2 (Hawker et al. 2022) (Table 4). We used two GRASS GIS modules: *r.slope.aspect* and *r.geomorphon*.

Table 4. Topographic metrics description.

Metric	Short description	Values	Reference
1. Elevation	Digital representation of elevations (or height) in meters through Digital Elevation Model (DEM).	Meters	Hawker et al. (2022)
2. Slope	Inclination from the horizontal stated in degrees	Degrees (0º to 90º)	Hawker et al. (2022)
3. Aspect	Direction that slopes are facing counterclockwise from East in degrees: 90 degrees is North, 180 is West, 270 is South, 360 is East	Degrees (0º to 360º)	Hawker et al. (2022)

4. Profile curvature	Curvature in the direction of steepest slope in 1/meters. A curvature of 0.05 corresponds to a radius of curvature of 20 meters and positive and negative values represent convex and concave forms, respectively	Units	Hawker et al. (2022)
5. Tangential curvature	Curvature in the direction of the contour tangent in 1/meters. A curvature of 0.05 corresponds to a radius of curvature of 20 meters and positive and negative values represent convex and concave forms, respectively	Units	Hawker et al. (2022)
6. Geomorphon	Classification and mapping of landform elements from a DEM based on the principle of pattern recognition (geomorphon)	Classes: flat (1), peak (2), ridge (3), shoulder (4), spur (5), slope (6), hollow (7), footslope (8), valley (9), pit (10)	Jasiewicz and Stepinski (2013)

Hydrological metrics

We calculated four hydrological metrics using a Digital Elevation Model (DEM) map from FABDEM v1.2 (Hawker et al. 2022) (Table 5). Due to the large extension, we first calculated these metrics for hydrological smaller basins using the HydroBASINS level 5 (Lehner and Grill 2013); after that we merged the results into single maps for the four metrics. We used two GRASS GIS modules to calculate the potential streams and springs: *r.watershed* and *r.stream.extract*, both with threshold = 100. With the potential streams and strings done, we deleted the lines and points, respectively, that overlap with masses of water from HydroLAKES (Messager et al. 2016) and official masses of water from three countries: Brazil (Instituto Brasileiro de Geografia e Estatística – IBGE; IBGE, 2021), Argentina (Instituto Geográfico Nacional – IGN; IGN, 2023) and Paraguay (Instituto Nacional de Estadística – INE; INE, 2023). Stream Euclidean distance was generated using *r.grow.distance* GRASS GIS module with metric = euclidean, and spring kernel was generated using *v.kernel* module with radius varying (50 m, 100 m, 150 m, 200 m, 250 m, 500 m, 750 m, 1000 m, 1500 m, 2000 m, 2500 m) and kernel = gaussian.

Table 5. Hydrological metrics description.

Metric	Short description	Values	Scale (buffer radius in meters)	Reference
1. Stream	Potential streams generated	0 and 1	None	Holmgren

	from DEM			(1994)
2. Stream distance	Euclidean distance from potential streams generated from DEM	Meters	None	Holmgren (1994)
3. Spring	Potential springs generated from DEM	0 and 1	None	Holmgren (1994)
4. Spring density	Density (kernel) of potential springs generated from DEM	Units	50, 100, 150, 200, 250, 500, 750, 1000, 1500, 2000, 2500	Okabe et al. (2009)

Anthropic metrics

We calculated 12 anthropic metrics represented by Euclidean distances outside (positive values) from roads, railways, protected areas, indigenous territories, and the grouped classes categories: pasture, temporary crop, perennial crop, forest plantation, urban areas, mining, and water (Table 1; Figure 2b). These metrics represented the approximation of human impact at the landscape scale. We used the *r.grow.distance* GRASS GIS module with metric = euclidean.

Table 3. Anthropic metrics description.

Metric	Short description	Values	Reference
1. Distance from roads	Euclidean distance from roads	Meters	Ribeiro et al. (2009)
2. Distance from railways	Euclidean distance from railways	Meters	Ribeiro et al. (2009)
3. Distance from roads and railways	Euclidean distance from roads and railways	Meters	Ribeiro et al. (2009)
4. Distance from protected areas	Euclidean distance from protected areas	Meters	Ribeiro et al. (2009)
5. Distance from indigenous territories	Euclidean distance from indigenous territories	Meters	Ribeiro et al. (2009)
6. Distance from the forest plantation	Euclidean distance from forest plantation	Meters	Ribeiro et al. (2009)
7. Distance from the pasture	Euclidean distance from pasture	Meters	Ribeiro et al. (2009)
8. Distance from the temporary crop	Euclidean distance from temporary crop	Meters	Ribeiro et al. (2009)
9. Distance from the perennial crop	Euclidean distance from perennial crop	Meters	Ribeiro et al. (2009)

10. Distance from the urban areas	Euclidean distance from urban areas	Meters	Ribeiro et al. (2009)
11. Distance from the mining	Euclidean distance from mining	Meters	Ribeiro et al. (2009)
12. Distance from the water	Euclidean distance from water (lakes and rivers)	Meters	Ribeiro et al. (2009)

Software

All the landscape, topographic, hydrological and anthropic metrics were processed using GRASS GIS 8.3 (Neteler et al. 2012) and R language 4.3 (R Core Team, 2023) with the aid of the *rgrass* package (Bivand, 2023). All landscape metrics were calculated using custom functions based on *LSMetrics* and translated to R (https://github.com/LEEClab/LS_METRICS; Niebuhr et al. *in prep.*).

4. Project personnel

None.

Class III. Data set status and accessibility

A. Status

1. Latest update

November 2023.

2. Latest archive date

November 2023.

3. Metadata status

Last updated in November 2023, version submitted.

4. Data verification

Last updated in November 2023, version submitted.

B. Accessibility

1. Storage location and medium

The original ATLANTIC SPATIAL data set can be accessed as supporting information to this Data Paper publication in Ecology. Updated versions and additional information are

available at the Open Science Framework (OSF) (https://doi.org/10.17605/OSF.IO/AJUMC) and code at GitHub (https://github.com/mauriciovancine/ATLANTIC-SPATIAL). We also created the R package *atlanticr* (https://mauriciovancine.github.io/atlanticr) which, in addition to facilitating access to other data papers from the Atlantic series, provides a table with all metrics and their information "atlantic_spatial" and a function to download rasters "atlantic_spatial_download()".

2. Contact persons

Maurício Humberto Vancine (mauricio.vancine@gmail.com), Bernardo Brandão Niebuhr (bernardo_brandaum@yahoo.com.br) or Milton Cezar Ribeiro (miltinho.astronauta@gmail.com).

3. Copyright restrictions

4. Proprietary restrictions

a. Release date

None.

b. Citation

Please, cite this data paper when the data are used in publications or teaching events.

c. Disclaimer(s)

None.

5. Costs

None.

Class IV. Data structural descriptors

The data set contains 1003 files. ATLANTIC_SPATIAL.csv contains a table describing the vector and raster files. The AF delimitation vector is available as Geopackage (.gpkg). The 500 rasters are available as GeoTiff (.tif) and TFW files (.tfw). ATLANTIC_SPATIAL.zip contains all rasters in a single compressed file with GeoTiff (.tif) and TFW (.tfw) files.

A. Data set file

1. Identity: ATLANTIC_SPATIAL.csv

2. Size: 20 columns and 502 rows records, including header row, 231 KB.

3. Format and storage mode: comma-separated values (.csv).

4. Header information: See column descriptions in section B.

5. Alphanumeric attributes: Mixed.

6. Special characters/fields: None.

7. Authentication procedures: None.

1. Identity: ATLANTIC_SPATIAL.zip

2. Size: 232 GB.

3. Format and storage mode: compressed file (.zip).

4. Header information: None.

5. Alphanumeric attributes: None.

6. Special characters/fields: None.

7. Authentication procedures: None.

B. Variable information

1) Table 1. **Information in the ATLANTIC SPATIAL data set**. Description of the fields related with the study site of the ATLANTIC_SPATIAL.csv.

Variable identify	Variable description	Levels	Example
id	Identification code for each metric	001-502	006
metric	Metric name	Detailed name of metric in text format	atlantic_spatial_forest_vegetation_fragment_area
metric_group	Group of metrics	anthropic, hydrological, landscape, topographic	landscape
metric_type	Detailed description of metric types	Detailed description of metric types in text format	fragment_area
metric_description	Detailed description of metrics	Detailed description of metrics in text format	forest vegetation fragment area
value	Metric values	Detailed metrics values in text and number	0.09 to infinity

		formats	
value_description	Detailed description of metric values	Detailed description of metric values in text format	area
unit	Unit of metrics	1/meters, angles in degrees, binary, categorical, discrete, hectares, meters, meters/hectares, proportion, unit, unitary	hectares
lulc_class	Land use and land cover class	forest_plantation, forest_vegetation, mining, multiple, natural_vegetation, pasture, perennial_crop, temporary_crop, urban_areas, water	forest_vegetation
edge_depth_m	Edge depth for different metrics in meters. Edge depth is the minimum distance at which cells are classified as edges, those that are further away are classified as cores	30-240	NA
gap_crossing_m	Gap-crossing for different metrics in meters. Gap-crossing considers the ability of an organism to cross non-habitat gaps, characterizing the distance to functional connectivity	60-600	NA
scale_buffer_radius_m	Scale for different metrics in meters. Scale is the radius of the buffer to which the moving window is rotated to impute the effect of different scales on landscape metrics	50-10,000	NA
resolution	Raster pixel width and height.	30	30
file_name	Metrics file name	Multiple metrics name files	006_atlantic_spatial_forest_vegetation_fragment_area.tif

link_drive_tif	Link to the .tif file on Google Drive	Multiple links	https://drive.google.com/file/d/14yxqKSNlLVgzONtpTozGhPje4yxeVDcU
link_drive_tfw	Link to the .tfw file on Google Drive	Multiple links	https://drive.google.com/file/d/1G7vjuQ-sfm-4E2InIkm2NlcET7PzJG4a
link_drive_gpkg	Link to the .gpkg file on Google Drive	Multiple links	https://drive.google.com/file/d/1P1NH14zW_OVLHG_jbnCuqhxSVBkkDL64
link_osf_tif	Link to the .tif file on Open Science Framework (OSF)	Multiple links	https://osf.io/download/6p9ub/
link_osf_tfw	Link to the .tfw file on Open Science Framework (OSF)	Multiple links	https://osf.io/download/kvtcq
link_osf_gpkg	Link to the .gpkg file on Open Science Framework (OSF)	Multiple links	https://osf.io/download/b2t6h/

C. Data anomalies

If no information is available, this was indicated by “NA”.

Class V. Supplemental descriptors

A. Data acquisition

1. Data forms or acquisition methods

None.

2. Location of completed data forms

None.

3. Data entry verification procedures

None.

B. Quality assurance/quality control procedures

None.

C. Related materials

None.

D. Computer programs and data-processing algorithms

None.

E. Archiving

1. Archival procedures

2. Redundant archival sites

F. Publications and results

Vancine et al. (2024) used part of this data set to describe the spatiotemporal landscape structure of AF.

G. History of data set usage

1. Data request history

None.

2. Data set updates history

None.

3. Review history

None.

4. Question and comments from secondary users

None.

CRediT authorship contribution statement

MHV: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing— original draft, Writing—review and editing. **BBN**:

Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing— original draft, Writing—review and editing. **RLM**: Conceptualization, Data curation, Investigation, Software, Writing—review and editing. **JEFO**: Conceptualization, Data curation, Writing—review and editing. **VT**: Data curation, Conceptualization, Writing—review and editing. **RB**: Data curation, Writing—review and editing. **RSCA**: Data curation, Writing—review and editing. **EMZ**: Data curation, Writing—review and editing. **VCS**: Data curation, Writing—review and editing. **JGRG**: Conceptualization, Data curation, Writing—review and editing. **CHG**: Data curation, Methodology, Software, Writing—review and editing. **MG**: Writing—review and editing. **MCR**: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Writing— original draft, Writing—review and editing.

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CAPÍTULO 3: Landscape structure as the predictor of anuran taxonomic and functional diversity in a highly threatened hotspot

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Landscape structure as a predictor of anuran taxonomic and functional diversity in a highly threatened hotspot

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Abstract

Context

Habitat loss and fragmentation are the primary drivers of biodiversity loss worldwide. Amphibians are particularly susceptible to environmental changes due to their unique morphological and ecological characteristics.

Objectives

In this study, we evaluated the impact of landscape structure on the taxonomic and functional diversity (TD and FD) of anurans in the Brazilian Atlantic Forest. We hypothesized that habitat split (the discontinuity between forest and aquatic habitats) would be the principal predictor of anuran TD and FD, given the need for aquatic environments for the reproduction of most anurans.

Methods

We analyzed 324 communities encompassing 274 anuran species and 12 functional traits to assess anuran TD (Taxonomic Richness of species with aquatic larvae—TRicA and Taxonomic Richness of species with terrestrial development—TRicT). FD was computed as Functional Richness—FRic, Functional Evenness—FEve, Functional Divergence—FDiv, and their respective Standardized Effect Sizes (SES).

Results

Our results indicated that habitat loss was the most important variable in explaining anuran TD, with negative and significant effects for both TRicA and TRicT. Contrarily, habitat fragmentation showed no significant effects on TD. For FD, habitat loss was the most plausible variable to explain SESFRic, negatively and significantly affecting it. FEve was explained by habitat split, which also showed a negative and significant relationship. FDiv was not explained by any landscape metric, although habitat fragmentation was as plausible as the null model.

Conclusions

Our results demonstrated that the amount and continuity of forest and aquatic habitats are crucial for maintaining anuran diversity in the Atlantic Forest. Conserving forest remnants and their connections to aquatic environments is essential for the functioning of both terrestrial and aquatic ecosystems.

Keywords

Tropics, Habitat fragmentation, Habitat split, Community ecology, Amphibians, Traits.

Introduction

Habitat loss and fragmentation due to land use and cover chances are the main causes of biodiversity loss worldwide (Chase et al. 2020; Davison et al. 2021). These modifications include the reduction of total habitat area (habitat loss), the subdivision of habitat into patches (habitat fragmentation), the deterioration of habitat quality (habitat degradation), and the introduction of other land cover class (usually anthropic) that replace the lost habitat (Haddad et al. 2015; Banks-Leite et al. 2020). The combined action of these processes generates direct and indirect effects on landscape structure, altering its composition and configuration, reducing available habitat area and increasing isolation and edge effects for some species (Fahrig 2003, 2017). These effects together alter landscape features, such as habitat quantity/quality and species permeability, which can impact multiple components of biodiversity, including taxonomic, genetic, phylogenetic and functional diversity in communities (Fahrig 2017; Fletcher et al. 2018; Fahrig et al. 2019).

Although most studies have demonstrated the effects of landscape modifications on the taxonomic diversity (TD) (Banks-Leite et al. 2014; Palmeirim et al. 2019; Püttker et al. 2020; Rios et al. 2021b), referring to the number or composition of species in an ecological community, a wide range of studies have also demonstrated these effects on the reduction of the functional diversity (FD) (Flynn et al. 2009; Mouillot et al. 2013; Nowakowski et al. 2017; Liu et al. 2018; Hatfield et al. 2018; Zambrano et al. 2019; Suárez-Castro et al. 2020). FD can be understood as the variability of species' traits (e.g., morphology or natural history) in relation to biodiversity responses to the environment—*response traits*, or its effects on ecosystem functioning—*effect traits* (Petchey and Gaston 2006). For example, habitat amount, patch size and landscape heterogeneity were the main predictors of bird FD based on morphology (e.g., body mass, hand-wing index, and gape width), diet, foraging behavior, reproduction, migration, and activity period (De Coster et al. 2015; Bovo et al. 2018; Matuoka et al. 2020; Bonfim et al. 2021; Fuzessy et al. 2024; Moreno et al. 2024). Patch size and habitat amount explained the FD of small, medium, and large mammal in terms of morphology (e.g., body mass, tail length, and locomotion form), behavior, diet, and environmental sensitivity (Magioli et al. 2015, 2021; Bovendorp et al. 2019; Rios et al. 2021a). Additionally, habitat amount, and edge effects explained the reduction in anuran FD linked to habitat and reproduction traits (Almeida-Gomes and Rocha 2015; Ferreira et al. 2016; Almeida-Gomes et al. 2019).

Amphibians are among the organisms most influenced by the environment characteristics, primarily due to their morphological, physiological and ecological attributes (Pough et al. 2015; Moreno-Rueda and Comas 2023). For instance, amphibians typically have small body sizes and limited capacities for dispersal and long-distance locomotion. They rely on cutaneous respiration, which generally requires high skin permeability, making them sensitive to minor changes in microclimatic conditions (Wells 2007; Moreno-Rueda and Comas 2023). Most amphibian species exhibit a biphasic life cycle (larval–aquatic and adult–terrestrial), with a high dependence on humidity and/or water availability for reproduction (Duellman and Trueb 1994). This habitat specificity often involves transitions between different habitat types and a high dependence on specific microhabitats for reproduction (Becker et al. 2007, 2010b). Consequently, landscape modifications are identified as one of the primary causes for the worldwide decline of amphibian populations (Cushman 2006; Grant et al. 2020; Green et al. 2020; Luedtke et al. 2023).

The Atlantic Forest harbors more than 720 species of amphibians, with over 500 species (about 70%) being endemic (Figueiredo et al. 2021). However, 46 species are currently threatened, mainly due to agricultural and urban expansion (Anunciação et al. 2024). Currently, only 23% to 26% of the forest's original extent remains, with 97% of the fragments being less than 50 ha, highly isolated (~800 m apart), and heavily impacted by roads and railways (Vancine et al. 2024). These factors have led to significant biodiversity and biomass loss (de Lima et al. 2020, 2024). Despite some stability and increases in forest cover, old forests have been replaced by younger forests, likely resulting in a considerable decline in habitat quality (Rosa et al. 2021; Piffer et al. 2022). Given the high diversity and endemism of amphibians, the substantial loss, fragmentation, and conversion of habitats and microhabitats suggest that a significant portion of this diversity is at risk of extinction (Haddad and Prado 2005; Almeida-Gomes and Rocha 2014). This extensive habitat loss and fragmentation may directly or indirectly drive species population declines (Becker et al. 2010b; Toledo et al. 2023; Anunciação et al. 2024), potentially compromising the functioning of both aquatic and terrestrial ecosystems (Whiles et al. 2006; Nowakowski et al. 2017).

Amphibians exhibit a wide range of reproductive modes globally (Nunes-de-Almeida et al. 2021), many of which are present in the Atlantic Forest (Haddad and Prado 2005). This diversity of reproductive strategies is a fundamental aspect of their life history and species diversity in this biome (Haddad and Prado 2005). Different reproductive guilds respond variably to landscape modifications (Almeida-Gomes and Rocha 2015; Ferreira et

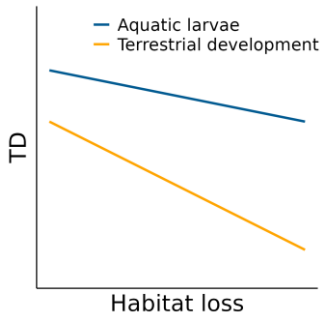
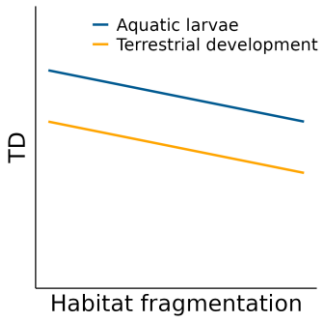
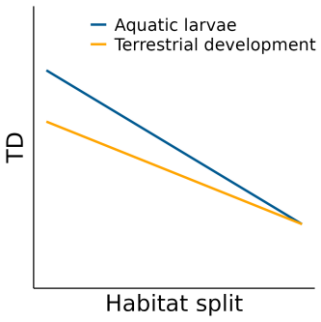
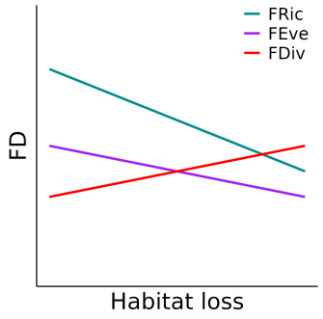
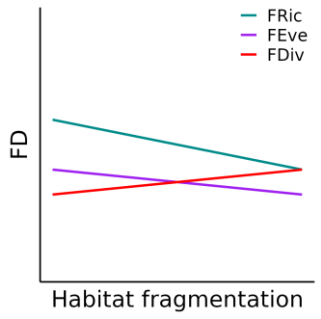
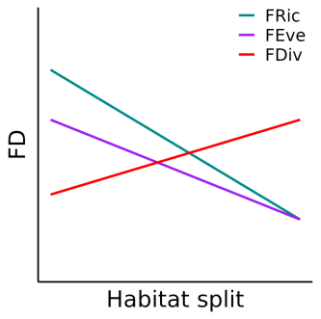
al. 2016). Species with aquatic reproduction, involving an aquatic larval stage (tadpoles) and a terrestrial, forest-dependent adult stage, need to migrate between these habitats at various life stages. They are particularly affected by two landscape features: the discontinuity between terrestrial and aquatic habitats—*habitat split* (Becker et al. 2007, 2010b, a), and the shortest distance from the fragment to the water bodies—*split distance* (Fonseca et al. 2013; Lion et al. 2014). Reproductive guilds that lack a larval stage or whose adults do not migrate between different habitats are more influenced by patch size and edge effects, such as species that reproduce in bromeliads or directly in the litter (Dixo and Martins 2008; Dixo and Metzger 2010; Ferreira et al. 2016). Therefore, understanding how communities are structured in fragmented landscapes in terms of TD and FD requires considering the different responses of reproductive guilds to various landscape metrics (Werner et al. 2007; Todd et al. 2009; Almeida-Gomes and Rocha 2014, 2015; Nowakowski et al. 2017; Almeida-Gomes et al. 2022).

Our study aimed to understand the effect of landscape structure on amphibian TD and FD for response traits in the Brazilian Atlantic Forest (BAF). Previous studies have described the effects of habitat loss and fragmentation on amphibian diversity at local scales, highlighting the impact of habitat amount and habitat split on TD and FD (e.g., Almeida-Gomes *et al.* 2019; Becker *et al.* 2007, 2010b, a). Multiple studies have shown that habitat split is the main spatial predictor of anuran richness, abundance, and diseases (e.g., *Batrachochytrium dendrobatidis*) in aquatic guilds within fragmented landscapes (Becker *et al.* 2007, 2010a, b, 2023; Becker & Zamudio 2011; Lion *et al.* 2014; but see Pereira Ramalho *et al.* 2022). Thus, we expected the same predictor to explain the TD and FD components in a highly endangered and fragmented biodiversity hotspot such as the BAF. Here, we scale up these analyses to comprehend how these factors predict the anuran TD (Taxonomic Richness of species with aquatic larvae—TRicA, and Taxonomic Richness of species with terrestrial development—TRicT), and FD (Functional Richness—FRic, Functional Evenness—FEve, and Functional Divergence—FDiv).

We hypothesize that for TD, following Becker *et al.* (2007), habitat split would be the main predictor of TRicA, as these species need to migrate between terrestrial and aquatic habitats multiple times during their life cycle. For TRicT, habitat loss would be the main predictor, since these species do not need to migrate and can complete their life cycle by reproducing in bromeliads or directly in leaf litter (Table 1). Our hypothesis for FD indices was that habitat split would be the main factor influencing these indices. Given that habitat split significantly affects species by selecting those with specific movement, habitat, and

reproductive guilds, we also expect an environmental filter for functional traits associated with these characteristics. Following Suárez-Castro *et al.* (2020), we predict a decrease in FRic (amount of space of functional traits), as a larger habitat split increases the environmental filtering of certain functional traits. We also predict a reduction in FEve (functional trait space equitability), as greater habitat split should lead to more uniformity in functional traits due to similar responses to landscape changes. Finally, we expect an increase in FDiv (functional trait space divergence), as greater habitat split is likely to cause greater displacement of functional traits within the functional space of all communities, with species responding similarly to the same effects of landscape changes (Table 1).

Table 1. Predictions for anuran taxonomic diversity (TD) and functional diversity (FD) in relation to habitat loss, habitat fragmentation, and habitat split in the Brazilian Atlantic Forest.

Diversity	Habitat loss	Habitat fragmentation	Habitat split
TD			
FD			

Methods

Amphibian communities

We used amphibian community data from the ATLANTIC AMPHIBIANS (Vancine et al. 2018). We filtered this data set to include only samples collected after 1985,

with available sampling information, and from locations with data in the FBDS data available (see *LULC and hydrological data* section for details). We excluded samples from dunes and *Eucalyptus* spp. plantations to ensure analyses were restricted to natural vegetation habitats. We also excluded samples with less than twelve months of sampling effort to capture at least part of both the dry and rainy seasons (Becker et al. 2007, 2010a), and those with fewer than six species due to functional analysis limitations (see *Taxonomic and functional diversity metrics* section). For sites with multiple sampling events at the same coordinates, we retained only the most recent sample. To ensure uniformity, we excluded samples from islands and areas far from the core BAF distribution (see maps in Muylaert et al. 2018). This BAF delimitation encompasses wide longitudes (35º W to 58º W), latitudes (3° S to 33° S) and elevations (0 to 2900 m a.s.l.) (Marques et al. 2021). After initial filtering, we retained 355 communities out of the 1163 available (30%). We included only species with valid names, excluding entries labeled as "species" (sp.), "several species" (spp.), "confer" (cf.), "affinis" (aff.), and "group" (gr.), and omitted the exotic species *Aquarana catesbeiana* to avoid interference in the functional analysis. We updated the species taxonomy following FROST 6.2 from November 2023 (Frost, 2023) using the R package *AmphiNom* (Liedtke 2019). This process resulted in 392 species out of a total of 534 (73%), with 349 up-to-date, 40 updated, 3 not found, and 6 duplicated, leaving 389 species (73%). After further filtering for communities with more than six species, 333 communities (29%) and 388 species remained. We also filtered for species with complete data in our trait data set (see *Traits data* section). The final data set consisted of 324 anuran communities (28%), with 5,171 records of 274 species, sampled between 1992 and 2014 (Fig. 1A; Fig. S1; Fig. S2). We tested whether sampling effort (months) and sampling methods (active, passive, and both) could affect TD and FD metrics, but we found low Kendall correlation values (Fig. S3; Table S1), so we did not consider them in our analyses.

LULC and hydrological data

We used two groups of covariates: landscape and hydrological geospatial data (Fig. 1B). For landscape data, we used Land Use and Land Cover (LULC) information from MapBiomas Brazil collection 8, which provides annual LULC data at 30-m spatial resolution from 1985 to 2022 (Souza et al. 2020). This data set was generated from a pixel-based random forest classifier of Landsat satellite images processed using Google Earth

Engine, with 32 LULC classes and an overall accuracy of 87.9% for the BAF (Souza et al. 2020). We convert the LULC maps into binary rasters (non-habitat/habitat, 0/1) for landscape analyses, defining habitat as all the classes considered "Forest" by MapBiomas: Forest Formation (class number 3), Savanna Formation (class number 4), Mangrove (class number 5), Floodable Forest (class number 6), and Wooded Sandbank Vegetation (*restinga*; class number 49).

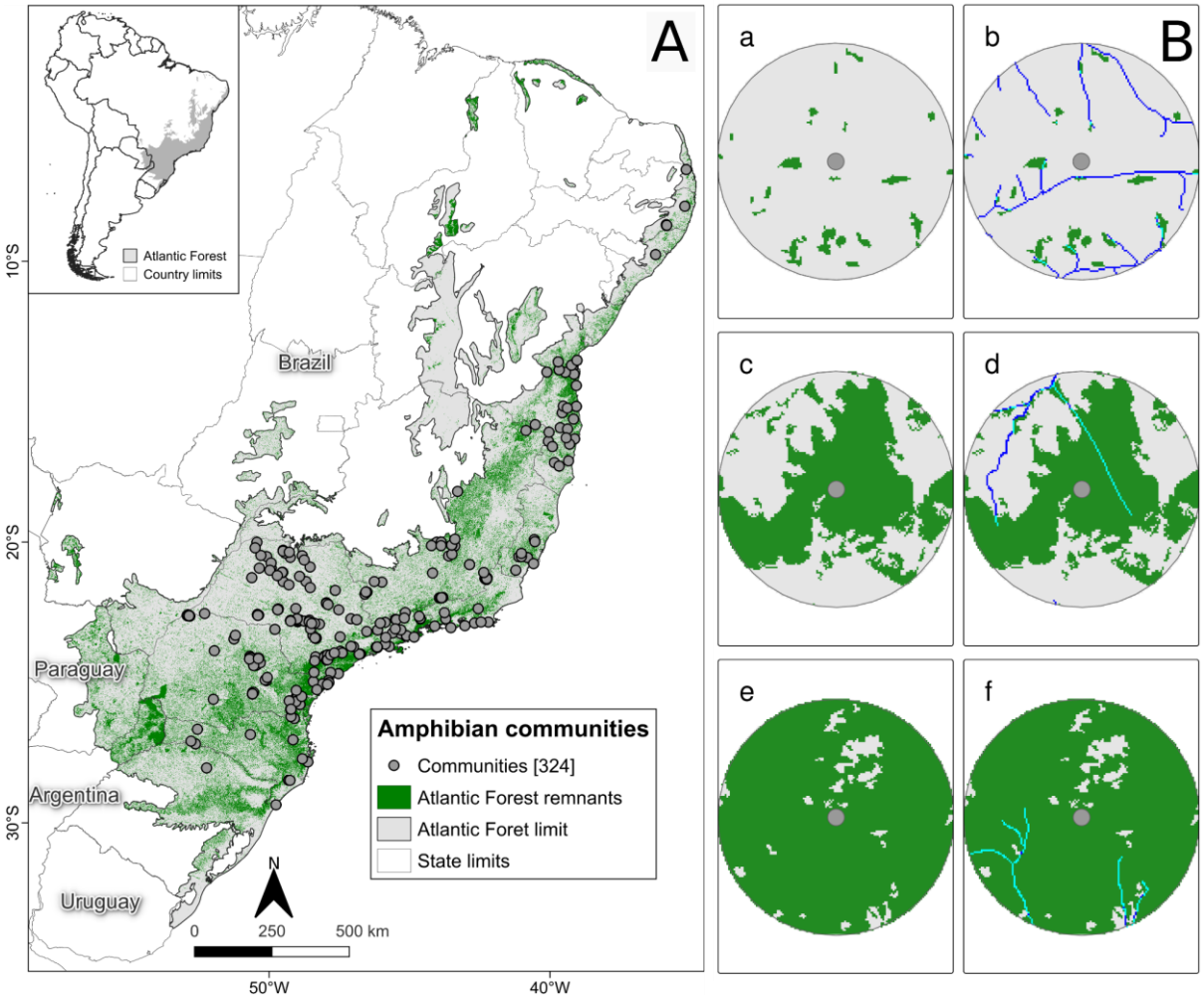


Figure 1. (A) Spatial distribution of 324 amphibian communities in the BAF. (B) Raster covariates for 2 km radius buffer: (a) high habitat loss, (b) high habitat split, (c) intermediary habitat loss, (d) intermediary habitat split, (e) low habitat loss, and (f) low habitat split. The colors represent: green (habitat), gray (non-habitat), dark blue (river without habitat overlap), and light blue (river with habitat overlap).

The hydrological data, representing simple rivers and bodies of water, were downloaded from the Brazilian Foundation for Sustainable Development ([Fundação Brasileira para o

Desenvolvimento Sustentável] FBDS; https://geo.fbds.org.br). These data were derived from official cartographic surveys and adapted using RapidEye images for vectorization at a 1:10,000 scale, with contours generated from the SRTM Digital Elevation Model (30 m/pixel) (details in Rezende et al. (2018)). We removed overlapping simple rivers to improve the accuracy of the hydrological tracings.

Covariates

The covariates, comprising landscape metrics and habitat split, were calculated within a circular buffer with a 2 km radius around each amphibian community, consistent with the approach used in previous studies (Almeida-Gomes and Rocha 2014; Lion et al. 2014; Püttker et al. 2020; Magioli et al. 2021). Landscape metrics included one metric for habitat loss (100 minus percentage of habitat) and habitat fragmentation (average perimeter-to-area ratio), calculated using the R package *landscapemetrics* (Hesselbarth et al. 2019). *Habitat split* was determined as the percentage of hydrography pixels (single rivers) that did not overlap with habitat pixels (Becker et al. 2007, 2010a). This metric was computed using functions from the R package *terra* (Hijmans 2024). We reproject all vector and raster maps for each amphibian community for different UTM zones within BAF delimitation (Fig. S4) and rasterize them for a 30 m pixel resolution. Fig. 1 illustrates these rasters for some example landscapes.

Trait data

We utilized trait data from ATLANTIC AMPHIBIAN TRAITS (Vancine et al., *in prep.*), also employed in Anunciação et al. (2023). This data set comprises morphological and ecological traits of amphibians across the entire BAF. Following the framework of Functional Trait Groups (FTGs) and other traits for amphibians (Tsianou & Kallimanis 2016, 2019, 2020; Vasconcelos *et al.* 2019), we select morphological and ecological traits from three groups, considered as *response traits*: morphological, reproductive, and habitat-related (Table 2).

Table 2. List of 12 morphological and ecological traits (including movement, reproductive and habitat-related) of anurans in the ATLANTIC AMPHIBIAN TRAITS data set for Functional Trait Groups (FTGs).

FTG	Trait	Type	Category	Unit/level	Ecological role
Morphological	Body size	Continuous	Quantitative	Millimeters	Movement
Morphological	Forelimb	Continuous	Quantitative	Millimeters	Movement
Morphological	Hindlimb	Continuous	Quantitative	Millimeters	Movement
Morphological	Toe disc	Categorical	Nominal	Presence, absence	Climbing vegetation
Reproductive	Calling site	Categorical	Nominal	Bromeliad, forest_floor, others, stream_rivulet, swamp_or_pond	Life history
Reproductive	Oviposition	Categorical	Nominal	Carried_adult, nest, plant, terrestrial, water	Life history
Reproductive	Egg type	Categorical	Nominal	Aquatic, arboreal, terrestrial	Life history
Reproductive	Tadpole nutrition	Categorical	Nominal	Direct_development, endotrophic, exotrophic	Life history
Habitat-related	Adult habitat	Categorical	Nominal	Forested_areas, open_areas	Habitat utilization
Habitat-related	Adult habit	Categorical	Nominal	Aquatic, arboreal, cryptic, arboreal and cryptic, rheophilic, terrestrial	Habitat utilization
Habitat-related	Tadpole habit	Categorical	Nominal	Running_water, still_water, terrestrial, froglet, no_tadpole	Habitat utilization
Habitat-related	Locomotion mode	Categorical	Nominal	Hopper, hopper_burrower, jumper, swimmer, walker_hopper, walker_hopper_burrower, walker_jumper	Habitat utilization

For all individual morphological measurements, we averaged the values, adjusted for body size to mitigate allometric effects, and standardized them using the “decostand” functional of R package *vegan* (Oksanen et al. 2022). Morphological traits included body size (snout-vent length—SVL), forelimb length (sum of humerus, radioulna, and hand lengths), hindlimb length (sum of femur, tibiofibula, tarsus, and foot lengths), and presence

of toe disc used as a response trait for anuran movement, migration, and dispersion across landscapes (Emerson 1988). Reproductive traits encompass life history aspects such as calling site, oviposition, egg type, and tadpole nutrition, related to the reproductive characteristics of anuran species. Habitat-related traits comprised adult habitat, adult habit, tadpole habit, and locomotion mode, reflecting the behavior of anuran species in habitat utilization. We included only species with complete traits information to avoid inaccurate estimates resulting from missing data (Johnson et al. 2021).

Taxonomic and functional diversities metrics

TD was computed as the sum of species within each amphibian community, with separate calculations for species with aquatic larvae (Taxonomic Richness of species with aquatic larvae—TRicA), and those with terrestrial development species (Taxonomic Richness of species with terrestrial development—TRicT) following Becker *et al.* (2007). FD was assessed according to the protocol outlined by Palacio *et al.* (2022), employing the framework implemented in the R package *mFD* (Magneville et al. 2022). Initially, we categorized each trait based on the information provided in the 'Category' column of Table 2. Subsequently, we utilized the “funct.dist” function to calculate a dissimilarity trait matrix between species, with dissimilarity values indicating the divergence between pairs of species based on functional traits. As both continuous and categorical traits were present, we applied a generalization of Gower's distance as the dissimilarity measure (Podani 1999). Next, we conducted a Principal Coordinates Analysis (PCoA) using the functional distance between species, facilitated by the “quality.spaces” function. Additionally, we employed this function to assess the quality of spaces constructed based on the number of principal coordinates, measuring the absolute deviation between trait-based distance and distance in the PCoA-based space (Maire et al. 2015). Our analysis indicated that six PCoA axes were optimal for calculating functional diversity indices (Fig. S5). Examination of the contributions of PCoA axes for traits revealed that the first three axes accounted for 76% of the variation (Fig. S7).

Then, we utilized “alpha.fd.multidim” to calculate three alpha functional diversity metrics: Functional Richness (FRic), Functional Evenness (FEve), and Functional Divergence (FDiv). The comprehensive analysis of these metrics enables the assessment of species responses to various habitat disturbances, as each functional diversity metric represents multiple functional aspects of species within communities (Mouchet et al. 2010;

Mouillot et al. 2013). FRic describes the amount of functional trait space occupied by species, ranging from zero to infinity; higher FRic values indicate greater breadth or volume of functions in a community. FEve indicates how equitable the functional trait space is occupied by the species, ranging from zero to one; higher FEve values indicate that different functions are equally represented in a community. FDiv measures the distance of species from the center of the functional trait space, ranging from zero to one; higher FDiv values indicate that the most abundant species have distinct traits (Mammola et al. 2021).

To account for potential influences of species richness on certain FD metrics, we standardized effect sizes (SES). We employed a simulation approach to generate a null model with expected values by chance while maintaining a constant number of species. To achieve this, the incidence matrix of community data was randomized using the "independent swap" algorithm, preserving species occurrence frequency and richness, which resulted in 999 random communities per site utilizing the "randomizeMatrix" function from the R package picante (Kembel et al. 2010). Subsequently, we calculated the FD metrics for each simulation, and used the means and standard deviations to compute the SES for each metric, following the formula: SES = [(observed values - mean of expected values)/standard deviation of expected values] (Gotelli and McCabe 2002; Botta-Dukát 2018). Negative SES values indicate lower observed FD compared to what would be expected by chance, suggesting stronger environmental filtering and greater species similarity. Conversely, positive SES values indicate higher observed FD than expected by chance, proposing stronger niche complementarity and lower functional similarity among species (Petchey and Gaston 2007).

Data analyses

To minimize redundancy among the TD and FD indices, we calculated the Kendall correlation between them (Xu et al. 2013). The analysis revealed that FRic had a high correlation with TRicA ($\tau = 0.64$; $p < 0.01$) and TRicT ($\tau = 0.55$; $p < 0.01$), so we only considered SESFRic, which had a low correlation with the TD metrics (Fig. S6). The correlation values between FEve and SESFEve ($\tau = 0.78$; $p < 0.01$), and FDiv and SESFDiv ($\tau = 0.76$; $p < 0.01$) were high; therefore, we chose to continue the analyses with only FEve and FDiv (Fig. S6). We also analyzed the correlation between the predictor variables using the Kendall correlation. Despite the high correlation between habitat loss

and habitat split ($\tau = 0.65$; $p < 0.01$) (Fig. S7), collinearity among the explanatory variables was low, with the variance inflation factor (VIF) less than four (Dormann et al. 2013). Following Becker *et al.* (2007), we maintained both variables.

We used Generalized Linear Mixed Models (GLMM) to relate the TD and FD indices with landscape metrics employing the R package *glmmTMB* (Brooks et al. 2017). All predictor variables were scaled and standardized using the "scale" function. Spatial autocorrelation was controlled using a spatial exponential covariance structure () and a random term for each anuran community: exp(coords + 0 | id), where *coords* are longitude and latitude coordinates and *id* are the community identification (Beale et al. 2010; Zuckerberg et al. 2012, 2020). We built four models for each TD and FD index with isolated variables: (1) TD/FD ~ 1 [null model] + exp(coords + 0 | id); (2) TD/FD ~ habitat loss + exp(coords + 0 | id); (3) TD/FD ~ habitat fragmentation + exp(coords + 0 | id); and (4) TD/FD ~ habitat split + exp(coords + 0 | id). For TD (TRicA and TRicT), we used the "poisson" error family; for FD, we used two families: "t_family" for SESFRic and "beta_family" for FEve and FDiv. Assumptions of residuals (uniformity, variance, outliers, dispersion, zero inflation, and spatial autocorrelation) were tested using the R package *DHARMa* (Hartig 2022), with diagnostics indicating that all models met these assumptions.

Finally, we compared these models using the Information Theoretical Approach with different methods through Akaike Information Criterion (AICc, delta AICc, and weight AICc) (Burnham and Anderson 2002). Models that were equally plausible were selected as those with delta AICc < 2 and weight AICc > 0.1 (Burnham and Anderson 2002), using the R package *bbmle* (Bolker and R Development Core Team 2023). Predictions were plotted using R package *marginaleffects* (Arel-Bundock 2024). To further explore the effect of landscape structure on functional traits, we analyzed the Kendall correlation between the mean value or dominant categorical trait in each anuran community and landscape metrics.

Results

Taxonomic diversity

Of the 274 anuran species in our data set, 32 were classified as having terrestrial development reproduction. The mean total richness was 15.96 ± 8.01 SD (range 7–51),

mean aquatic larvae richness (TRicA) was 15 ± 7.22 SD (range 5–46), and mean terrestrial development (TRicT) was 0.96 ± 1.48 SD (range 0–7). In nearly 70% of landscapes (n = 187), no terrestrial development species were present. The most frequently occurring species were *Dendropsophus minutus*, *Physalaemus cuvieri*, *Boana faber*, *Scinax fuscovarius*, *Boana albopunctata*, *Leptodactylus latrans*, *Leptodactylus fuscus*, *Rhinella ornata*, *Leptodactylus mystacinus*, and *Rhinella icterica*, each found in more than 100 landscapes. Conversely, 51 species were recorded in only a single landscape. These species belong to the families: Hylidae (n = 17), Brachycephalidae (n = 10), Leptodactylidae (n = 9), Craugastoridae (n = 3), Hylodidae (n = 3), Phyllomedusidae (n = 3), Cycloramphidae (n = 2), Microhylidae (n = 2), Bufonidae (n = 1), and Odontophrynidae (n = 1).

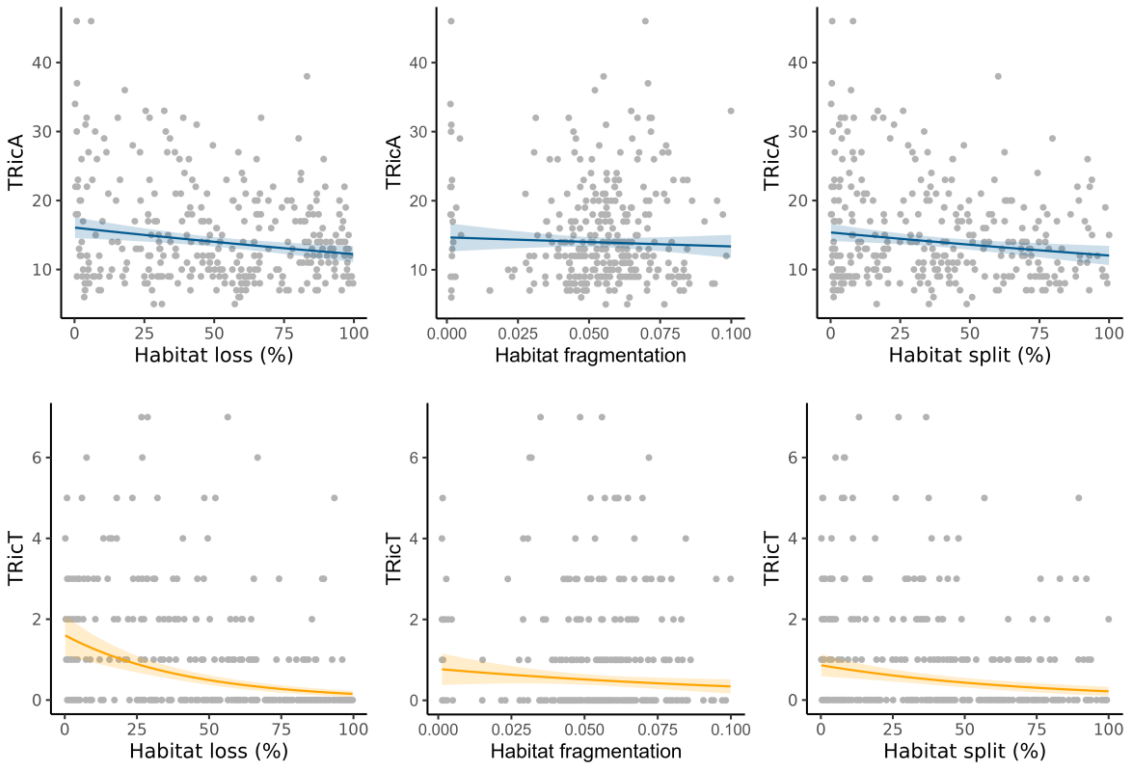


Figure 2. Predicted responses of anuran taxonomic diversity to the taxonomic richness of species with aquatic larvae (TRicA) and terrestrial development (TRicT). Shaded areas represent the 95% confidence interval.

Habitat loss was the most important variable in explaining anuran TD, for both TRicA (w_i = 0.8) and TRicT (w_i = 0.99) (Fig. 2, Table 3). This variable showed negative and significant effects on TRicA (slope = -0.08±0.02, $p < 0.01$) and TRicT (slope = -0.72±0.1, $p < 0.01$) (Fig. 2, Table S2). Contrarily, habitat fragmentation showed no

significant effects, and habitat split, despite not being a plausible model, had negative and significant effects on TRicA (slope = -0.07±0.03, $p < 0.01$) and TRicT (slope = -0.41±0.10, $p < 0.01$) (Fig. 2, Table S2).

Table 3. Model selection based on a candidate set of models predicting anuran species taxonomic diversity indices. Abbreviations: TRicA: taxonomic richness of species with aquatic larvae, TRicT: taxonomic richness of species with terrestrial development, K: number of parameters, LL: log likelihood, AICc: Akaike's Information Criterion corrected for small samples, ΔAICc: difference in Akaike's Information Criterion, and w_i: Akaike weight.

Model	*K*	LL	AICc	ΔAICc	w_i
TRicA ~ null	3	-1051.6	2109.2	10.41	0.009
TRicA ~ habitat loss	**4**	**-1046.1**	**2100.3**	**0.00**	**0.801**
TRicA ~ habitat frag.	4	-1051.3	2110.7	8.92	0.004
TRicA ~ habitat split	4	-1047.6	2103.2	2.93	0.185
TRicT ~ null	3	-438.6	883.2	56.94	<0.001
TRicT ~ habitat loss	**4**	**-409.1**	**826.3**	**0.00**	**0.999**
TRicT ~ habitat frag.	4	-436.9	882.1	55.76	<0.001
TRicT ~ habitat split	4	-429.8	867.7	41.37	<0.001

Functional diversity

For FD components, habitat loss was the most plausible variable to explain SESFRic ($w_i = 0.99$), negatively and significantly affecting it (slope = -0.10±0.02, $p < 0.01$) (Fig. 3, Table S2). FEve was explained by habitat split ($w_i = 0.99$), which also showed a negative and significant relationship (slope = -0.15±0.02, $p < 0.01$) (Fig. 3, Table S2). FDiv was not explained by any landscape metric, although habitat fragmentation was as plausible as the null model (Table 4).

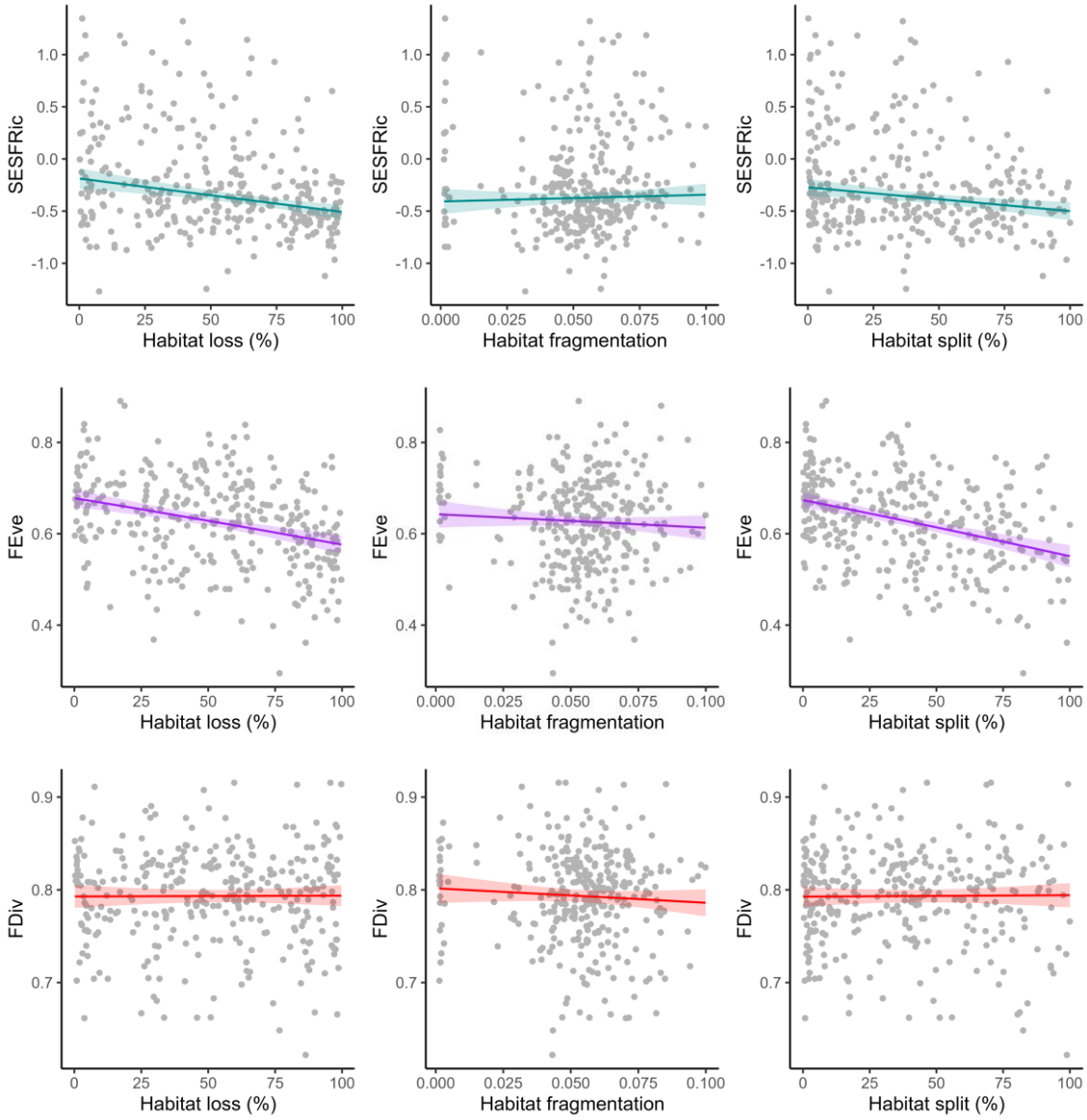


Figure 3. Predicted responses of anuran functional diversity to standardized effect sizes functional richness (SESFRic), functional evenness (FEve) and functional divergence (FDiv). Shaded areas represent the 95% confidence interval.

An exploratory analysis of functional traits in relation to landscape metrics demonstrated some patterns, which align with landscape structure (Fig. S8, Table S3). There was a positive relationship between body size and habitat loss ($\tau = 0.23$; $p < 0.01$) and habitat split ($\tau = 0.17$; $p < 0.01$); forelimb length had a negative relationship with habitat loss ($\tau = -0.38$; $p < 0.01$) and habitat split ($\tau = -0.27$; $p < 0.01$); and hindlimb length showed a negative relationship with habitat loss ($\tau = -0.10$; $p < 0.01$). Toe disc presence was higher in locations with less habitat loss ($\tau = -0.16$; $p < 0.01$) and habitat split ($\tau = -0.14$; $p < 0.01$). Calling site in "forest floor" and "bromeliad" showed were higher in sites

with less habitat loss ($\tau = 0.10$; $p = 0.03$) and habitat split ($\tau = 0.10$; $p = 0.02$). Adults with "forest habitat" were more prevalent in landscapes with lower habitat loss ($\tau = 0.34$; $p < 0.01$) and habitat split ($\tau = 0.24$; $p < 0.01$). Locomotion mode "hopper" was higher in landscape with higher habitat split ($\tau = -0.10$; $p = 0.03$). However, habitat fragmentation did not show a clear relationship with any of the functional traits (Fig. 8, Table S3).

Table 4. Model selection based on a candidate set of models predicting anuran species functional diversity indices. Abbreviations: SESFRic: standardized effect sizes functional richness, FEve: functional evenness, FDiv: functional divergence, K: number of parameters, LL: log likelihood, AICc: Akaike's Information Criterion corrected for small samples, ΔAICc: difference in Akaike's Information Criterion, and w_i: Akaike weight.

Model	*K*	LL	AICc	ΔAICc	*wi*
SESFRic ~ null	3	-200.0	406.1	20.02	<0.001
SESFRic ~ habitat loss	**4**	**-188.9**	**386.1**	**0.00**	**0.996**
SESFRic ~ habitat frag.	4	-199.9	407.8	21.71	<0.001
SESFRic ~ habitat split	4	-194.6	397.3	11.15	0.004
FEve ~ null	4	295.0	-581.9	43.71	<0.001
FEve ~ habitat loss	5	311.9	-613.7	11.94	0.003
FEve ~ habitat frag.	5	295.7	-581.2	44.52	<0.001
FEve ~ habitat split	**5**	**317.9**	**-625.7**	**0.00**	**0.997**
FDiv ~ null	**4**	**508.1**	**-1008.1**	**0.00**	**0.42**
FDiv ~ habitat loss	5	508.1	-1006.0	2.05	0.15
FDiv ~ habitat frag.	**5**	**508.7**	**-1007.2**	**0.82**	**0.28**
FDiv ~ habitat split	5	508.1	-1006.0	2.03	0.15

Discussion

Our results indicated that habitat loss and habitat split were more important variables than habitat fragmentation in explaining TD and FD of anuran communities in the BAF. Our hypotheses were partially corroborated for TD: contrary to our expectations,

habitat loss, rather than habitat split, was the most plausible variable for explaining TRicA; consistent with our initial prediction, habitat loss was also the most important variable explaining TRicT. For FD, our hypotheses were again partially corroborated: habitat loss, rather than habitat split, was a more plausible variable in explaining SESFRic; confirming our hypothesis, habitat split was more influential for FEve; and contrary to our expectations, no relationship was found between FDiv and landscape metrics. These findings align with other studies demonstrating the negative effects of landscape changes on the TD and FD of various animal groups in the Atlantic Forest at large spatial scales, including birds (Bovo et al. 2018; Bonfim et al. 2021, 2024; Fuzessy et al. 2024), mammals (Magioli et al. 2015, 2021; Bovendorp et al. 2019; Palmeirim et al. 2019; Rios et al. 2021b, a), and multiple taxa (Püttker et al. 2020).

However, our findings do not align with studies conducted at smaller spatial scales. For instance, Becker *et al.* (2007), Becker et al. (2010), and Lion *et al.* (2014) identified habitat split and split distance as more critical factors in explaining species number and the abundance of anurans with aquatic larval reproduction in the Atlantic Forest. Additionally, our results contrast with those of Prado & Rossa-Feres (2014), who found that pond hydroperiod and area, rather than split distance, were key factors for anuran species richness and occupancy in the Atlantic Forest. Similarly, from studies in the Cerrado Biome. Ramalho *et al.* (2022) reported that habitat fragmentation, irrespective of habitat loss and habitat split, was more significant for predicting taxonomic diversity, functional diversity, and the abundance of terrestrial anurans. Nevertheless, Ramalho *et al.* (2021) indicated that habitat split was an important predictor at the landscape scale, along with forest habitat amount for arboreal anuran species and the number of water bodies for terrestrial anuran species.

Functional diversity indices showed a negative relationship with landscape metrics, potentially indicating significant consequences for ecosystem functioning as communities respond to changes in landscape structure (Flynn et al. 2009; Mouillot et al. 2013; Liu et al. 2018; Zambrano et al. 2019). SESFRic was lower in landscapes with high habitat loss, indicating a reduced functional trait space and suggesting that habitat loss acts as an environmental filter, increasing species similarity and leading to the absence of some specialist species (Mouillot et al. 2013). FEve was lower in landscapes with high habitat split, suggesting reduced equitability of functional trait space. This could indicate that habitat split acts as a significant filter for certain traits, leading to species co-occurrence (Mouillot et al. 2013). FDiv was not related to landscape metrics, possibly indicating no

displacement of functional traits within the functional space of all communities and no extreme trait values differing from the central values of the communities (Mouillot et al. 2013). This finding for FDiv is consistent with other studies in which landscape metrics did not explain functional diversity for birds at local scales (Matuoka et al. 2020; Manzoli et al. 2024), and with a theoretical study (Suárez-Castro et al. 2020).

Landscape composition metrics, such as habitat loss and habitat split, showed different correlations with various traits, which help explain the functional diversity indices results. Traits related to movement and dispersion indicated that landscapes with less forest habitat and lower connectivity between forest and aquatic habitats have species that are larger with smaller locomotor limbs, correlating with the "hopper" locomotion mode, once these species tend to move in small jumps (Emerson 1988; Pough et al. 2015). Habitat-related and reproductive traits showed that species in landscapes with greater habitat loss and habitat split had adaptations to forest vegetation. Toe disc presence was higher in landscapes with less habitat loss and split, indicating an association with climbing vegetation (Pough et al. 2015). Calling sites on the "forest floor" and "bromeliad" were more common in areas with less habitat loss and split, suggesting that these environments support more species for reproduction (Haddad and Prado 2005). As expected, adults associated with "forest habitat" were more prevalent in landscapes with lower habitat loss and split, confirming environmental filtering effects (Almeida-Gomes et al. 2016b; Almeida-Gomes et al. 2019; Püttker et al. 2020; Almeida-Gomes et al. 2022). These findings suggest that decreases in SESFRic and FEve are linked to strong environmental filtering due to habitat loss and split, particularly affecting species' movement and habitat use, as described by several studies (Becker et al. 2007, 2010a; Lion et al. 2014).

Despite the controversial results regarding habitat split observed in our study and other studies (e.g., Prado & Rossa-Feres (2014), Ramalho *et al.* (2022)), our findings support the Habitat Amount Hypothesis (Fahrig 2013), which suggests that species diversity can be predicted solely by the total percentage of habitat surrounding sampling sites. Our results confirm a linear trend of TD and FD loss with increasing habitat loss. Similar trends for TD and FD have been reported in other studies on anurans in the BAF at the local scale (Almeida-Gomes and Rocha 2015; Almeida-Gomes et al. 2016a; Ribeiro et al. 2018; Almeida-Gomes et al. 2019; Anunciação et al. 2021). However, numerous studies at the local scale in the BAF have also highlighted the importance of landscape configuration in predicting anuran diversity and abundance. Key factors include landscape connectivity (Almeida-Gomes and Rocha 2014), patch size (Almeida-Gomes et al. 2016b),

edge effects (Ferreira *et al.* 2016; but see Dixo & Martins 2008 and Lipinski et al. 2018), and matrix effect and fragmentation (Dixo and Metzger 2010). Therefore, it is crucial to consider both landscape composition metrics and metrics that describe landscape configuration.

Another reason why split habitat was not the main predictor of anuran TD and FD is that our species list differs from those used in other studies, which often analyze specific guilds of communities. For example, Becker *et al.* (2007) and Lion *et al.* (2014) analyzed the effects of habitat split and split distance, respectively, only for species with a leaf-litter habit. They did not consider species belonging to the Hylidae family, which are generally associated with forest habits. Additionally, these two studies used a pitfall trap sampling method, which tends to sample a particular part of the community: species living in the leaf litter. Other studies have conducted analyses that separate species with different habitat preferences, considering both the total community and the community composed only of forest species (Almeida-Gomes et al. 2016b; Almeida-Gomes et al. 2019; Püttker et al. 2020; Almeida-Gomes et al. 2022). Incorporating these factors into analyses could improve our understanding of community responses to landscape structure. As highlighted by Almeida-Gomes *et al.* (2019) and Fuzessy *et al.* (2024), analyzing the TD and FD of birds and frogs in the Atlantic Forest can provide more comprehensive insights.

We also note a terminological inconsistency regarding the definition of "habitat split". Becker *et al.* (2007) define "habitat split" as "the percentage of the total stream length that does not overlap with forest cover". In a theoretical study, Fonseca *et al.* (2013) defined "split distance" as the "shortest distance from the fragment to the river", a definition later used by Lion et al. (2014) to support empirical results. Some studies refer to "split distance" as "habitat split" (e.g., Prado & Rossa-Feres 2014 and Ramalho et al. 2021), which can cause confusion in interpreting the results, as "habitat split" is a metric of landscape composition, whereas "split distance" is a metric of landscape configuration. In this study, we used "habitat split" as defined by Becker *et al.* (2007), focusing on landscape composition, specifically the percentage of overlap between forest and streams. However, testing our hypotheses with the "split distance" metric could improve our predictions, and resolve the issue of high correlation between habitat loss and habitat split metrics. As highlighted by Becker et al. (2007), individuals need to disperse across landscapes, moving between forest and aquatic habitats to complete their life cycle. Therefore, we would expect community responses to be more closely associated with these landscape features, as our functional diversity metrics incorporated functional traits related

to movement and dispersal, such as body size, length of locomotor limbs, and mode of locomotion. Furthermore, expanding the "split distance" metric to incorporate matrix quality (Lion et al. 2014), landscape resistance (Covarrubias et al. 2021), and multiple habitat graphs (Savary et al. 2024), as well as the presence and distance from other lentic water bodies (e.g., lakes and ponds), could be integrated into a more accurate landscape configuration metric.

In addition, other variables focused on aquatic habitat and topography, such as stream density and slope (Ribeiro et al. 2018), and pond duration and size (Prado and Rossa-Feres 2014; Almeida-Gomes et al. 2016a), can be used to explain anuran community composition. In the Cerrado and at a local scale, aquatic habitat cover, the number of aquatic patches, and aquatic habitat isolation (Silveira et al. 2023), as well as the seasonality of these aquatic habitats (temporary and permanent ponds), seem to influence amphibian diversity (With et al. 2024). Other studies at a larger scale have focused on how climate conditions, climate change, and phylogenetic relationships have affected amphibian functional diversity in the BAF (Campos et al. 2017, 2019; Lourenço-de-Moraes et al. 2019; Anunciação et al. 2023; Fontana et al. 2023). Therefore, landscape metrics focused on aquatic habitat and environmental predictors such as topography and climate could be used to explain anuran diversity in the BAF.

Moreover, other spatial scales could be employed to calculate landscape metrics in analyses to identify the "scale of effect" using a multi-scale approach (Jackson and Fahrig 2012, 2015; Miguet et al. 2016). It is possible that our hypotheses can be revisited, as the scales of analysis of the landscape surrounding sampling sites varied between studies that tested the effects of habitat loss and habitat split. These scales ranged from radius buffers of 100 m (Almeida-Gomes et al. 2016a), 200 m (Ribeiro et al. 2018), 1,000 m (Prado and Rossa-Feres 2014), 2,000 m (Almeida-Gomes and Rocha 2014; Lion et al. 2014), to 7,500 m Becker *et al.* (2007). Thus, a multi-scale analysis could be a fundamental approach to finding the appropriate spatial scale for landscape metrics on diversity (Suárez-Castro et al. 2018, 2022), and improving the interpretation of the effects of landscape features on anuran diversity (Denoël and Lehmann 2006; Almeida-Gomes and Rocha 2014; Moraga et al. 2019; Sauer et al. 2022).

Exploring the same data set in different ways can yield more detailed insights into the effects of landscape changes on amphibian communities. For example, conducting the same analysis with community abundance data, which may be more sensitive to landscape modifications (Becker et al. 2007, 2010a; Lion et al. 2014), could provide additional

perspectives, despite this data representing only 30% of the original amphibian community data (Vancine et al. 2018). Additionally, analyses involving Structural Equation Modeling (SEM) could address the complexity of factors determining species diversity by testing direct and indirect causal effects with a series of dependent and independent variables that may be correlated (Becker et al. 2007; Bovendorp et al. 2019). Furthermore, analyses of other components of diversity, such as beta diversity, can reveal differences in community composition related to the partitioning (nestedness and turnover) of TD (Baselga 2012) and FD (Villéger et al. 2013), as already demonstrated for bird (Morante-Filho et al. 2016), mammal (Beca et al. 2017), and anuran (Gangenova et al. 2018; Almeida-Gomes et al. 2019) communities in the BAF. Other approaches, such as Hierarchical Modeling of Species Communities (HMSC) (Ovaskainen et al. 2017), can offer new perspectives and better elucidate the effects of landscape changes by considering species-specific responses and their relationships with functional traits and phylogenetic relationships, as has been done for mammals (Magioli et al. 2021) and birds (Bonfim et al. 2024) in the BAF.

Our study is the first to demonstrate the negative effects of landscape change on multiple components of anuran diversity at a large scale in the BAF. Although preliminary, our results clearly show the detrimental impacts of habitat loss and habitat split on the reduction of TD and FD in anuran communities within this biome. The BAF has less than 23% forest cover, with 97% of its fragments being less than 50 hectares and highly isolated (average isolation of 830 meters) (Vancine et al. 2024). Additionally, only 14.5% of fragments are stream-connected, with most being over 1 km away, and an average distance of 1208 meters (Lion *et al.* 2014). Extrapolating our results to the entire BAF suggests that most amphibian species are likely experiencing negative effects from habitat loss and habitat split.

Our findings underscore the importance of the quantity and connectivity of forest and aquatic habitats for maintaining various aspects of anuran diversity in the BAF, particularly concerning species movement and habitat use. Moreover, our results indicate that the ecological functions of amphibians may be compromised, as they play a crucial role in bridging terrestrial and freshwater ecosystems through their two-phase life cycle, which includes aquatic larvae and terrestrial post-metamorphic stages (Whiles et al. 2006, Hocking and Babbitt 2014, Cortes-Gomez et al. 2015, Nowakowski et al. 2017). Given that climate change and land cover change are major threats to amphibian diversity and diseases (Becker et al. 2016, 2017, 2023; Moura-Campos et al. 2021; Ceron et al. 2023; Anunciação et al. 2023), it is vital to further understand these issues to propose effective conservation

strategies. We conclude that the conservation of forest remnants and their connectivity with aquatic environments such as streams and lakes, represented by permanent preservation areas like riparian forests, is fundamental for ensuring the functioning of terrestrial and aquatic ecosystems. This will help maintain the ecological processes inherent to both ecosystems, as amphibians require the integrity of both habitats throughout their life cycle.

Data availability

Data used for this study are freely available on ATLANTIC AMPHIBIANS (Vancine et al., 2018), ATLANTIC AMPHIBIAN TRAITS (Vancine et al. *in prep.*), FBDS (https://www.fbds.org.br), and MapBiomas (https://brasil.mapbiomas.org). The data and R codes used are available at https://github.com/mauriciovancine/ms-landscape-structure-diversity-amphibians-atlantic-forest.

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Contributions

MHV: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Visualization, Writing—

original draft, Writing—review and editing. **BBN**: Conceptualization, Investigation, Methodology, Supervision, Writing—review and editing. **KSD**: Conceptualization, Investigation, Methodology, Writing—review and editing. **CGB**: Writing—review and editing. **TGS**: Conceptualization, Investigation, Methodology, Supervision, Writing—review and editing. **CFBH**: Writing—review and editing. **MCR**: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Supplementary Information

Figures

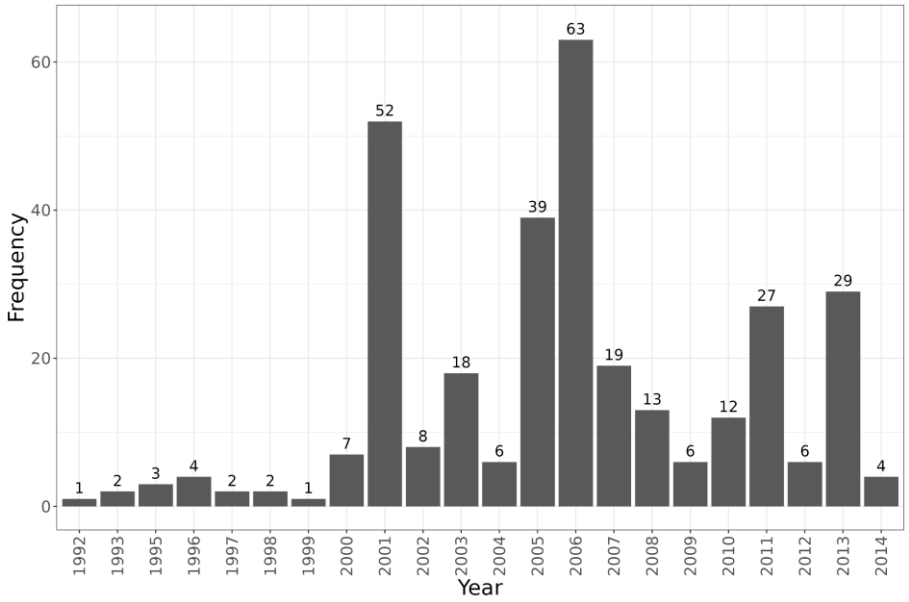


Figure S1. Temporal distribution of 514 amphibian communities over the years in the BAG.

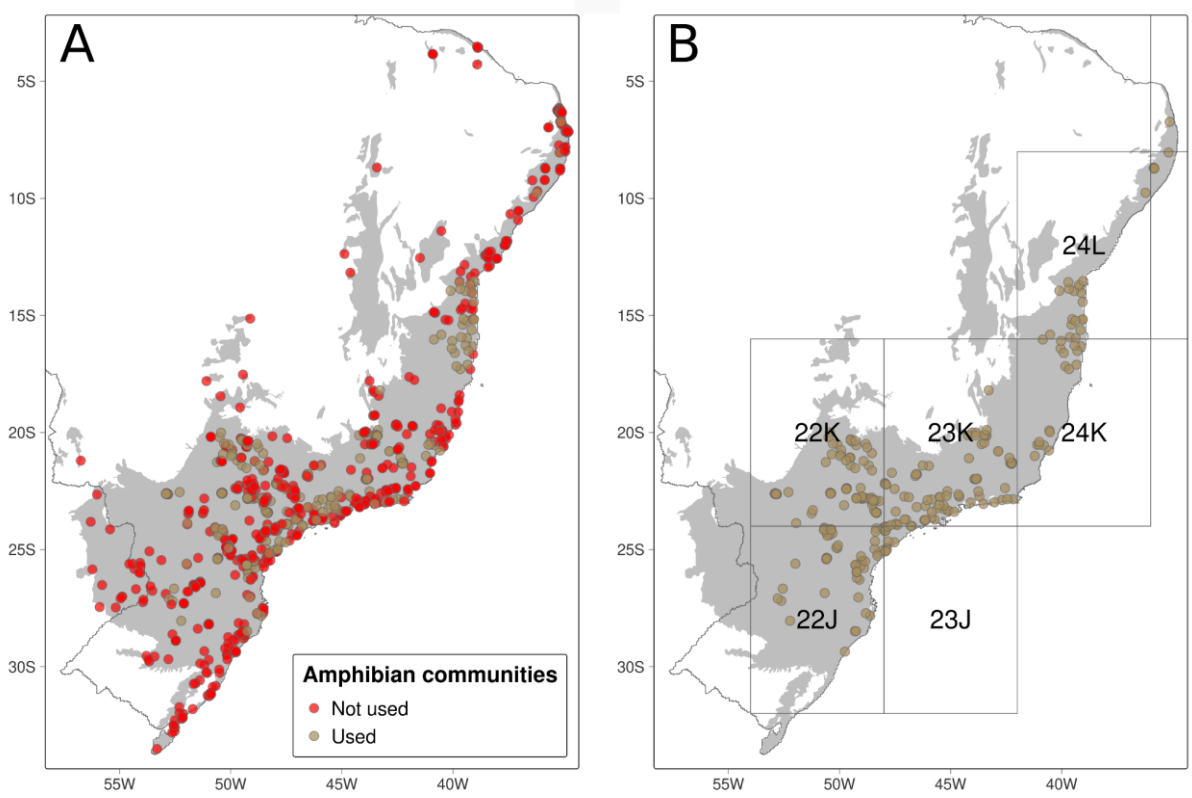


Figure S2. A. Spatial distribution of amphibian communities used (324) and not used (839) in the BAF. B. Spatial distribution of 324 amphibian communities and UTM zone

used to reproject the raster and vector geospatial data.

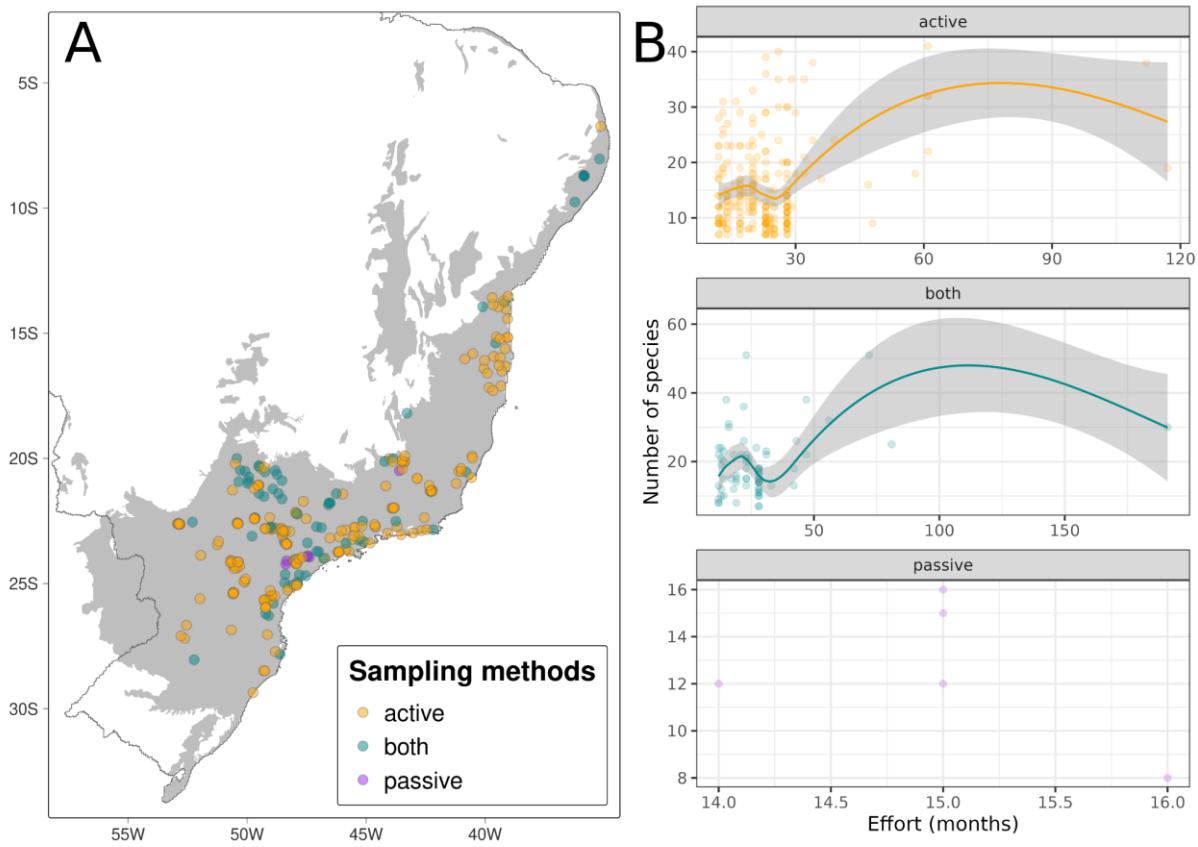


Figure S3. A. Spatial distribution of sampling methods amphibian communities (324) in the BAF. B. Number of species and sampling effort (months) for different sampling methods with LOESS adjustment.

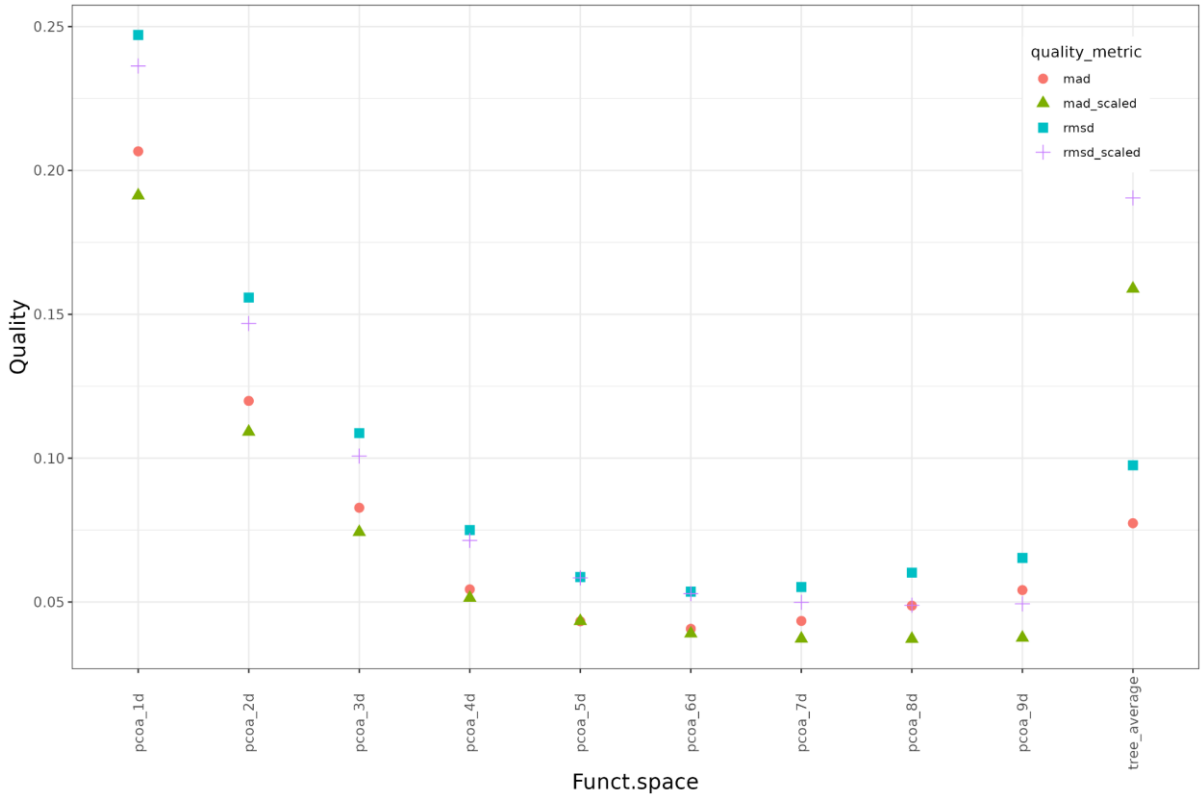


Figure S4. Quality of functional spaces from PCoA for traits axis.

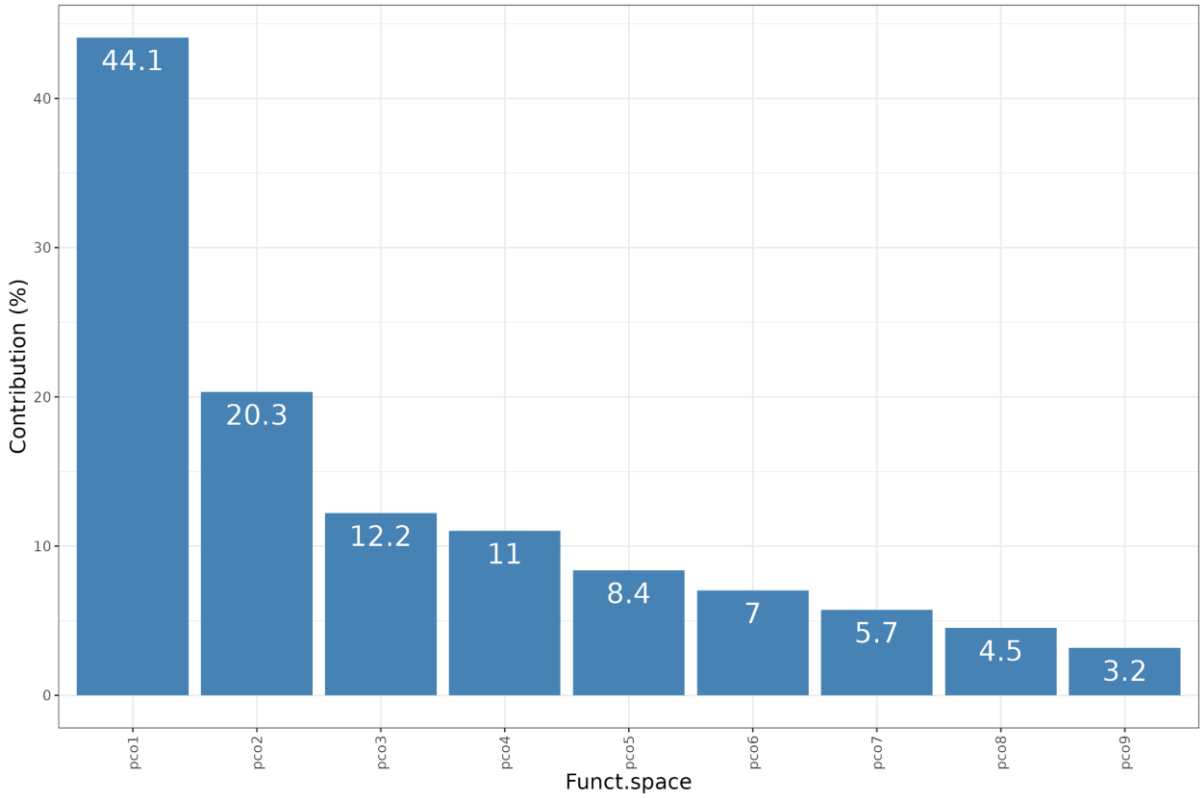


Figure S5. Contribution of functional space from PCoA traits axis.

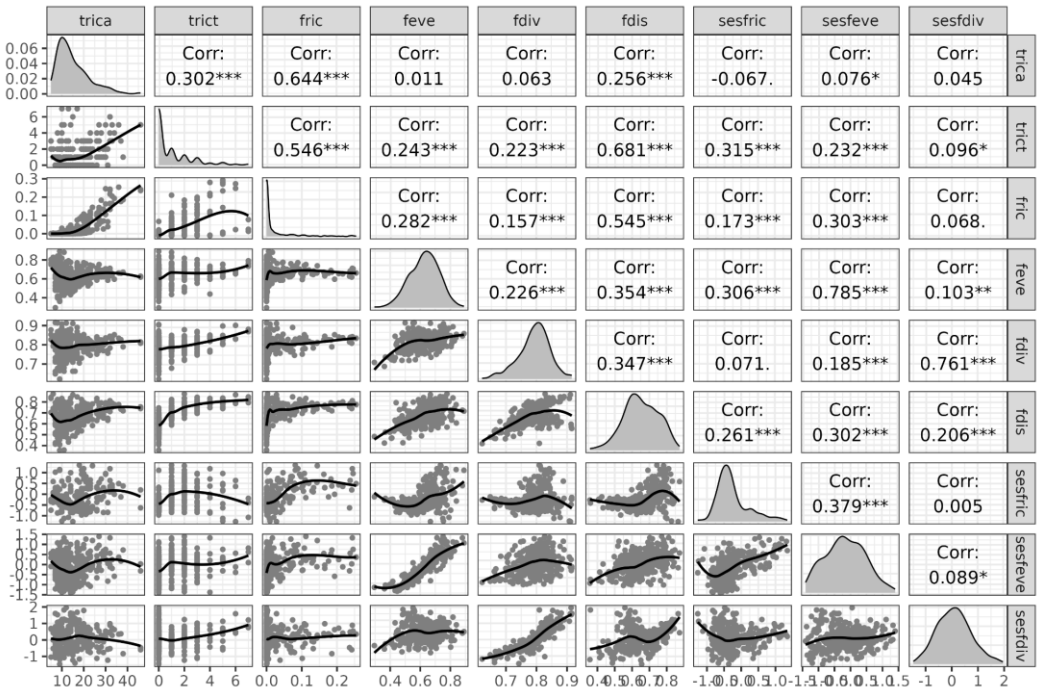


Figure S6. Correlation (Kendall) between taxonomic and functional diversities (response variables). Abbreviations: taxonomic richness of species with aquatic larvae (trica), taxonomic richness of species with terrestrial development (trict), functional richness (fric), functional evenness (feve), functional divergence (fdiv), standardized effect size of functional richness (sesfric), standardized effect size of functional evenness (sesfeve), and standardized effect size of functional divergence (sesfdiv).

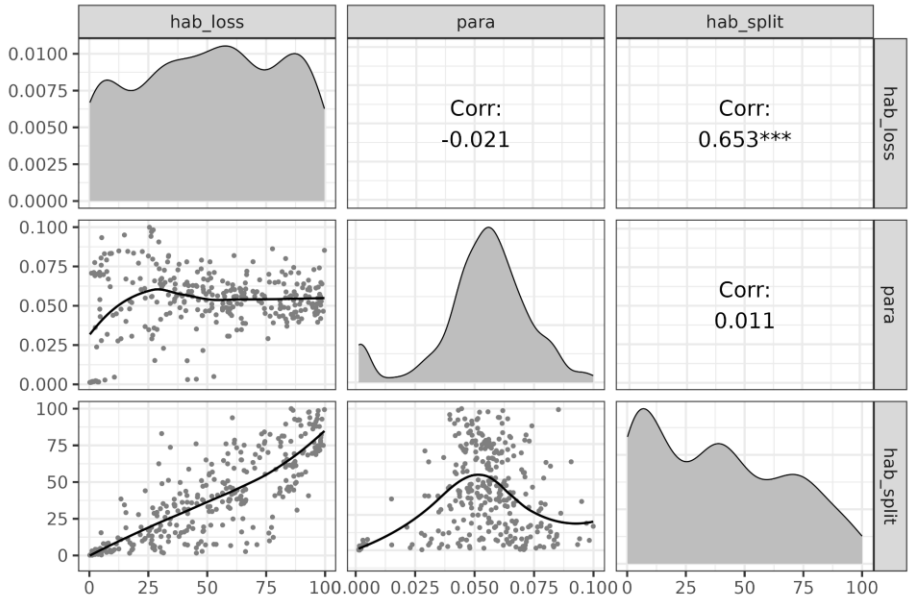
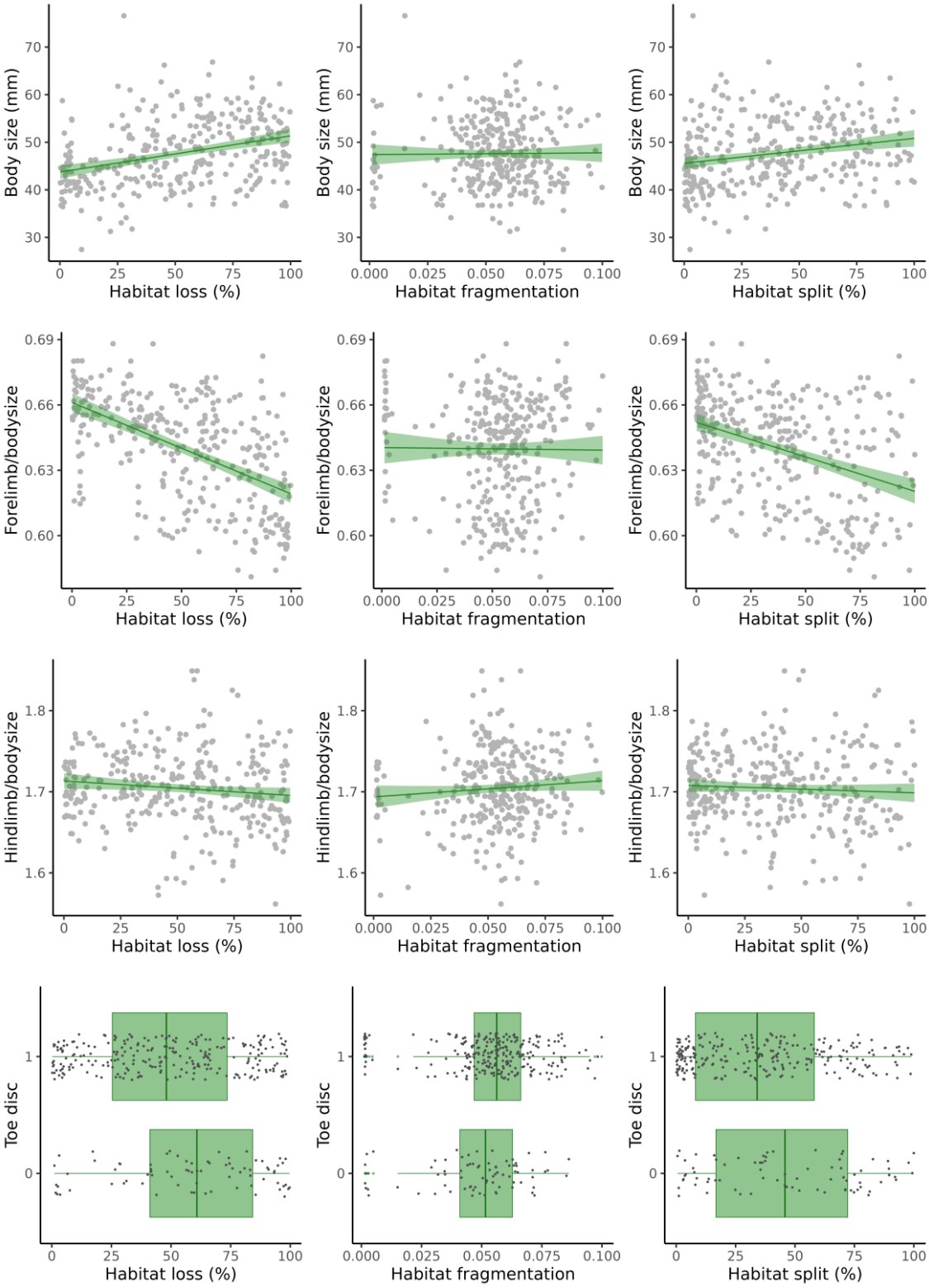
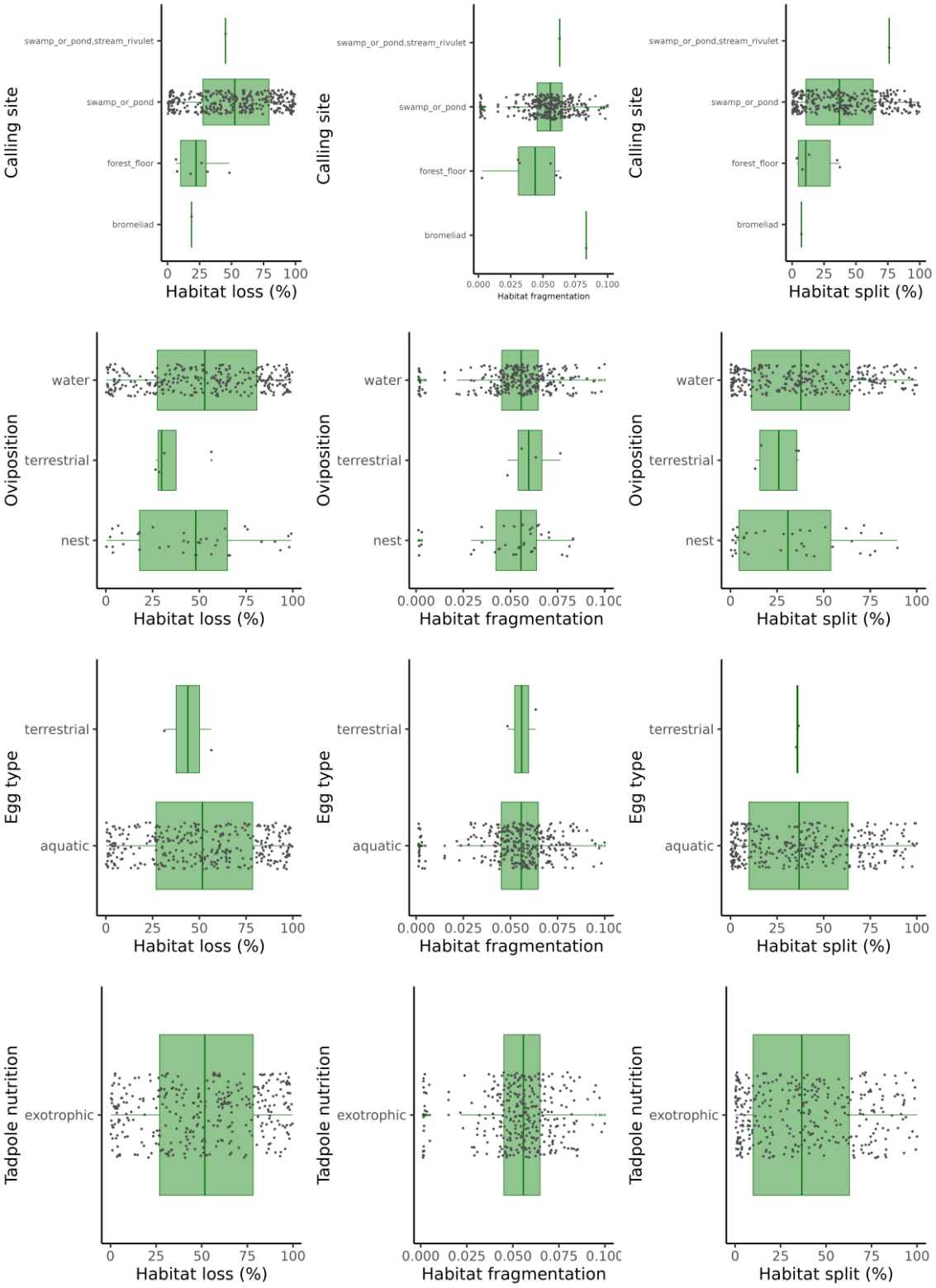


Figure S7. Correlation between covariates (predictor variables). Abbreviations: habitat loss (hab_loss), perimeter-area ratio (para), and habitat split (hab_split).


Body size (mm)
Habitat loss (%)
Habitat fragmentation
Habitat split (%)
Forelimb/bodysize
Hindlimb/bodysize
Toe disc


Calling site
swamp_or_pond,stream_rivulet
swamp_or_pond
forest_floor
bromeliad
Habitat loss (%)
Habitat fragmentation
Habitat split (%)
Oviposition
water
terrestrial
nest
Egg type
aquatic
Tadpole nutrition
exotrophic
0
25
50
75
100
0.000
0.025
0.050
0.075
0.100

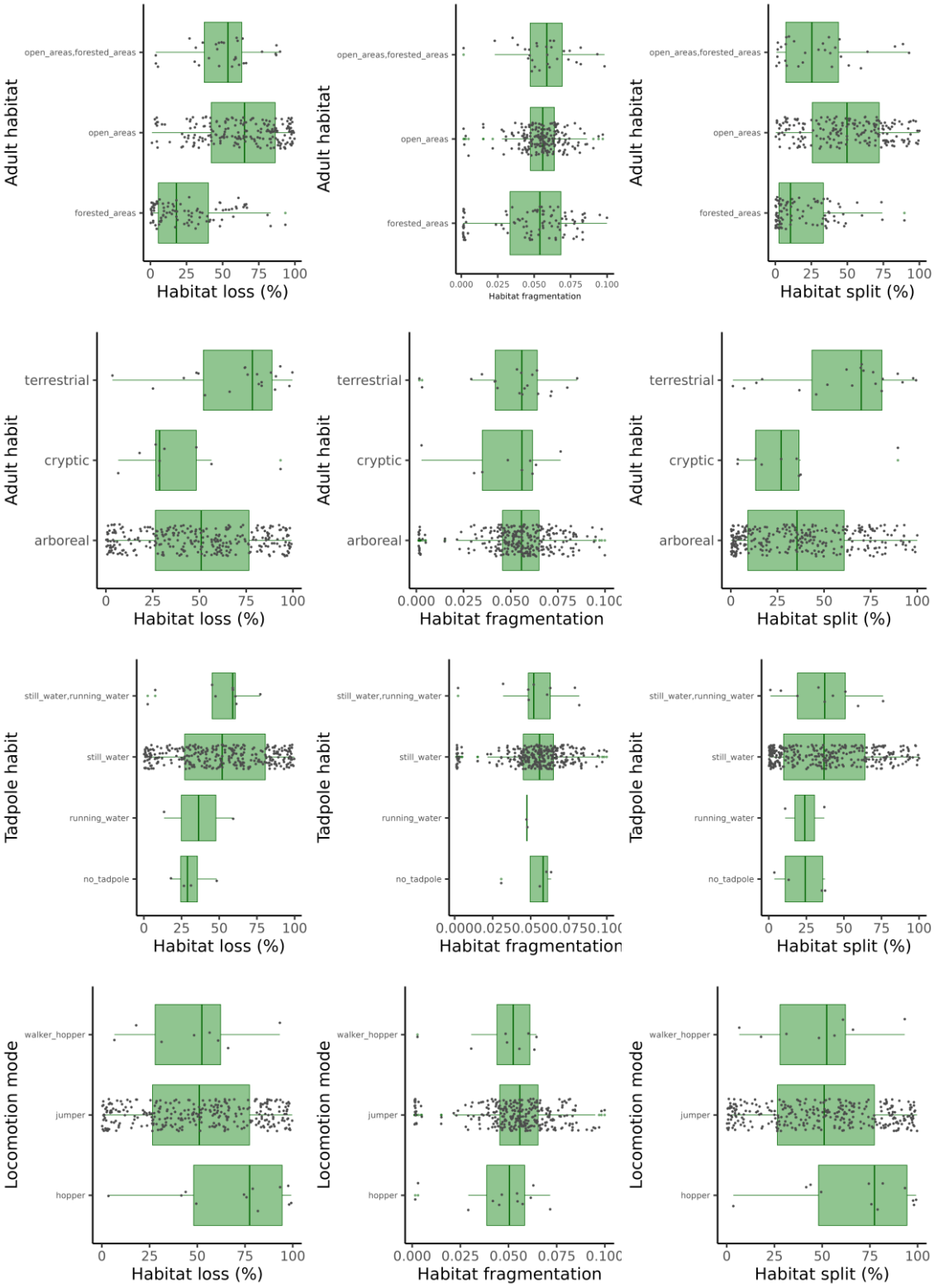


Figure S8. Relationship between landscape metrics and the average values or dominant categorical functional traits in each anuran community.

Tables

Table S1. TD and FD indices correlation (Kendall) with sampling effort and methods.

Diversity indices	Total effort method (n = 324)	Active effort method (n = 246)	Both effort method (n = 73)	Passive effort method (n = 5)
TRic	0.07	0.03	0.08	-0.25
TRicA	0.1	0.03	0.14	-0.12
TRicT	-0.03	0.06	-0.25	-0.27
FRic	0	0	-0.06	-0.12
FEve	-0.08	0	-0.23	0.36
FDiv	-0.01	0	-0.07	0.36
SESFRic	-0.05	0.02	-0.27	0.36
SESFEve	-0.05	0.02	-0.21	0.12
SESFDiv	-0.02	-0.02	-0.05	0.36

Table S2. Estimated parameters of the models that related the taxonomic and functional diversity indices of anuran species and the landscape structure.

Response variable	Predictor variable	Intercept	Slope	p
TRicA	Hab. loss	2.64±0.03	-0.08±0.02	<0.01
TRicA	Hab. frag.	2.64±0.03	-0.02±0.03	0.45
TRicA	Hab. split	2.64±0.03	-0.07±0.03	<0.01
TRicT	Hab. loss	0.73±0.13	-0.72±0.10	<0.01
TRicT	Hab. frag.	0.69±0.13	-0.16±0.09	0.07
TRicT	Hab. split	0.69±0.13	-0.41±0.10	<0.01
SESFRic	Hab. loss	-0.35±0.02	-0.10±0.02	<0.01
SESFRic	Hab. frag.	-0.37±0.02	0.01±0.02	0.54
SESFRic	Hab. split	-0.36±0.02	-0.07±0.02	<0.01
FEve	Hab. loss	0.52±0.02	-0.13±0.02	<0.01
FEve	Hab. frag.	0.52±0.02	-0.03±0.02	0.26

FEve	Hab. split	0.52±0.02	-0.15±0.02	<0.01
FDiv	Hab. loss	1.34±0.02	0.00±0.02	0.93
FDiv	Hab. frag.	1.35±0.02	-0.02±0.02	0.27
FDiv	Hab. split	1.34±0.02	0.00±0.02	0.87

Table S3. Correlation (Kendall) between the average values or dominant categorical functional traits and landscape metrics in each anuran community. Tadpole nutrition did not have data to explore the correlation.

Funcional trait	**Predictor variable**	**Kendall (τ)**	**p**
Body size	Habitat loss	0.23	< 0.01
Body size	Habitat frag.	-0.003	0.931
Body size	Habitat split	0.17	< 0.01
Forelimb/body size	Habitat loss	-0.38	< 0.01
Forelimb/body size	Habitat frag.	0.022	0.556
Forelimb/body size	Habitat split	-0.27	< 0.01
Hindlimb/body size	Habitat loss	-0.097	0.009
Hindlimb/body size	Habitat frag.	0.033	0.37
Hindlimb/body size	Habitat split	-0.047	0.206
Toe disc	Habitat loss	-0.16	< 0.01
Toe disc	Habitat frag.	0.089	0.05
Toe disc	Habitat split	-0.14	< 0.01
Calling site	Habitat loss	0.099	0.029
Calling site	Habitat frag.	0.033	0.464
Calling site	Habitat split	0.1	0.021
Oviposition	Habitat loss	0.08	0.076
Oviposition	Habitat frag.	0.02	0.652
Oviposition	Habitat split	0.078	0.083
Egg type	Habitat loss	-0.031	0.497
Egg type	Habitat frag.	0.033	0.464

Egg type	Habitat split	-0.003	0.945
Tadpole nutrition	Habitat loss	NA	NA
Tadpole nutrition	Habitat frag.	NA	NA
Tadpole nutrition	Habitat split	NA	NA
Adult habitat	Habitat loss	0.34	< 0.01
Adult habitat	Habitat frag.	0.056	0.2
Adult habitat	Habitat split	0.24	< 0.01
Adult habit	Habitat loss	0.053	0.236
Adult habit	Habitat frag.	-0.004	0.934
Adult habit	Habitat split	0.088	0.052

CAPÍTULO 4: ATLANTIC AMPHIBIAN TRAITS: a data set of morphological and ecological traits of amphibians in the Atlantic Forest

Maurício Humberto Vancine, Paula Ribeiro Anunciação, Kauã da Silva Duarte, Danilo Barêa Delgado, Nayara Helena Alecrim de Freitas, Luana Gabriela Nunes Damião, Milton Cezar Ribeiro, Célio Fernando Baptista Haddad

Tipo de manuscrito: Data paper

(EM PREPARAÇÃO SEGUINDO AS NORMAS DA REVITAS “ECOLOGY”)

ATLANTIC AMPHIBIAN TRAITS: a data set of morphological and ecological traits of amphibians in the Atlantic Forest

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Open Research statement

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Introduction

The lack of knowledge about the functional traits of species—Raunkiæran shortfall—represents a major challenge especially considering the growing number of studies focusing on functional diversity and the critical importance of this topic (Hortal et al. 2015, Gonçalves-Souza et al. 2023). Functional diversity reflects the variability of species' traits (e.g., morphology, physiology, or natural/life history) in relation to the biodiversity response to the environment or its effects on the ecosystem functioning (Petchey and Gaston 2006). Traits can be understood as *response traits*—how species respond to environmental gradients, and as *effect traits*—how species affect ecosystem functioning (Violle et al. 2007). When trait data are accessible, they are typically available at the species level, overlooking individual variance within species (Gonçalves-Souza et al. 2023), despite this variation being fundamental to several issues that use this approach (Cianciaruso et al. 2009, de Bello et al. 2011), such as communities structuring (de Bello et al. 2011, Violle et al. 2012), and species response to environmental factors (Albert et al. 2010). Most trait-based studies have primarily focused on plants than on animals (but see Schleuning et al. 2023), emphasizing response traits while neglecting intraspecific variation (Gonçalves-Souza et al. 2023). Among terrestrial vertebrates, amphibians stand out due to limited available data (Etard et al. 2020).

There are more than 8,700 species of amphibians (Class Amphibia) worldwide (Frost 2023). Despite being abundant in some terrestrial and freshwater ecosystems (Pough et al. 2015), amphibians are the most threatened group of vertebrates, with more than 40% of their species at risk of extinction (Luedtke et al. 2023). Amphibians are an interesting group for investigating trait-based approaches owing to their pivotal role in bridging terrestrial and freshwater ecosystems through their biphasic life cycle, which comprises aquatic larval and terrestrial post-metamorphic stages (Whiles et al. 2006, Hocking and Babbitt 2014, Cortes-Gomez et al. 2015, Nowakowski et al. 2017). Their roles in the ecosystem span from the predator-prey relationship, contributing to the storage and exchange of matter and energy, to serving as indicators of environmental changes (Cortes-Gomez et al. 2015, Díaz-García et al. 2017). However, to understand these ecosystem relationships, trait-based studies generally use morphological, continuous, and individual-level traits (Gonçalves-Souza et al. 2023). Despite recent efforts to bridge this knowledge gap (see Oliveira et al. 2017, Huang et al. 2023, Vera Candioti et al. 2023), information regarding these traits for amphibians remains scarce. Although there are several data sets

on species-level morphological and ecological traits for amphibians (e.g., Trochet et al. 2014, Oliveira et al. 2017, Neves et al. 2020, Huang et al. 2023, Vera Candioti et al. 2023), there is a paucity of information available documenting trait values at the individual-level, particularly in biodiverse forested regions, such as tropical ecosystems.

The Atlantic Forest of South America (AF) holds more than 700 species of amphibians, with over 500 species (about 70%) being endemic (Figueiredo et al. 2021), with 46 threatened species mainly due to agriculture and urban expansion (Anunciação et al. 2024). However, only around 23% of the forest remains due to urban progress and the expansion of pastures and agricultural frontiers. Furthermore, 97% of these forest fragments are smaller than 50 hectares and are highly isolated, with an average distance of approximately 800 meters between them (Vancine et al. 2024). Although the diversity of amphibians is both high and endemic, the extensive loss, fragmentation, and conversion of habitats and microhabitats suggest that a significant portion of this diversity is at risk of extinction (Haddad and Prado 2005, Almeida-Gomes and Rocha 2015, Nori et al. 2018, Bolochio et al. 2020). This significant level of habitat loss and fragmentation of AF may directly or indirectly contribute to the population declines among amphibian species (Becker et al. 2010, Carvalho et al. 2017, Rebouças et al. 2021), which can compromise the functioning of freshwater and terrestrial ecosystems (Whiles et al. 2006, 2013, Nowakowski et al. 2017). Therefore, gathering information about the functional characteristics of amphibians in the AF is crucial for evaluating their vulnerability to habitat loss, understanding their ecosystem roles, predicting responses to environmental changes, guiding restoration efforts, and prioritizing conservation actions.

Here, we present ATLANTIC AMPHIBIAN TRAITS, a data set comprising morphological and ecological traits at individual-level, encompassing measures from 2,489 individuals representing 357 anuran species distributed throughout the AF (Figure 1), along with traits at species-level for 533 species. The data set includes 12 individual-level morphological measurements: body size (snout-vent length—SVL), head width, head length, humerus, radioulna, hand, femur, tibiofibula, tarsus, foot, hindlimb, and forelimb from the Célio F.B. Haddad amphibian collection (CFBH) (Silva et al. 2021). Majority of the measurements include information about individuals collected: number of the voucher in the collection, state, municipality, locality, longitude, latitude, longitude approximate, latitude approximate, collection date, and collector. We also compiled 17 species-level ecological traits and information from literature: male body size (SVL), female body size (SVL), male body size (categorical), female body size (categorical), presence/absence of

toe disc, locomotion mode, activity, adult habitat, adult habit, tadpole habit, reproductive mode, calling site, oviposition, egg type, tadpole nutrition, abundance, toxicity, and endemism in the AF. All information came from Haddad et al. (2013) and Haddad and Prado et al. (2005) and our inference about toe disc presence and locomotion mode.

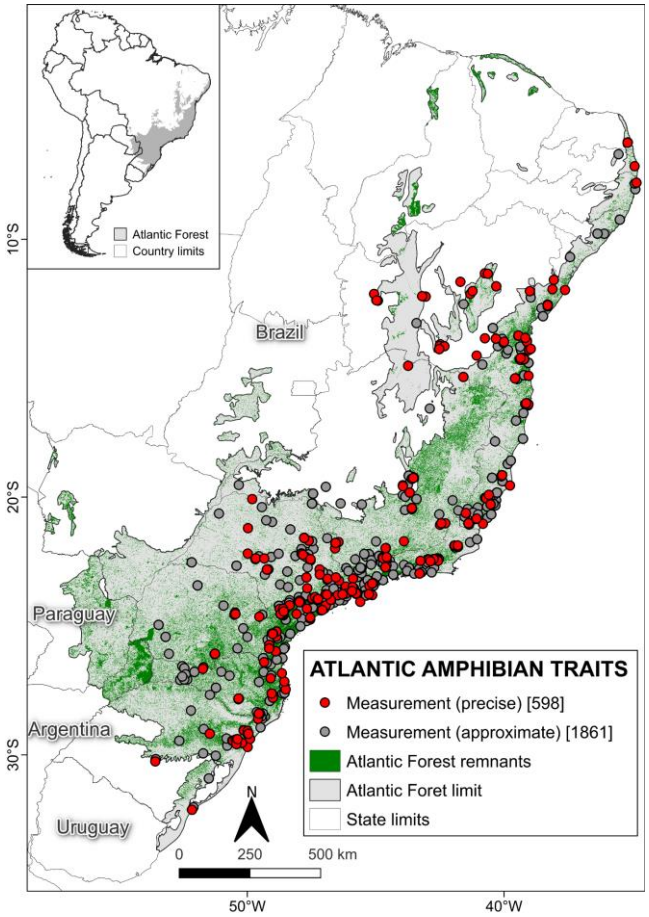

Figure 1. Original distribution of the Atlantic Forest in South America and current extent of its forest vegetation remnants in 2020. Dots represent individuals with morphological measurements taken at CFBH amphibian collection between 2016 and 2017 included in the ATLANTIC AMPHIBIAN TRAITS data set. Dark gray dots indicate measurements with approximate coordinates (1859), while red dots indicate measurements with precise coordinates (598) for 357 species (not all individuals have a collection location or coordinate available).

ATLANTIC AMPHIBIAN TRAITS is part of the ATLANTIC SERIES of data papers, a large initiative led by Brazilian researchers who have compiled hundreds of thousands of records documenting animal and plant species as well as environmental conditions in the AF. Data collection efforts span decades and have been synthesized in

numerous data papers (Bello et al. 2017, Bovendorp et al. 2017, Figueiredo et al. 2017, Lima et al. 2017, Muylaert et al. 2017, Gonçalves et al. 2018a, 2018b, Hasui et al. 2018, Vancine et al. 2018, 2023, Santos et al. 2018, Souza et al. 2019, Culot et al. 2019, Ramos et al. 2019, Rodrigues et al. 2019, Silva et al. 2022, Boscolo et al. 2023). We believe ATLANTIC AMPHIBIAN TRAITS represents a major effort to compile individual anuran traits for the Neotropical region, filling an important gap in the knowledge about individual and species variation and distribution of anuran morphological and ecological traits. Thus, this data set can assist in the development of new research on anthropogenic and climate change impacts on the functional diversity component of anurans in the AF. Furthermore, these data can also help address other gaps in amphibian studies, as pointed out by Haddad et al. (2022): life-history trait variation, disease transmission, community assembly, biogeography, and population forecasting.

METADATA

Class I. Data set descriptors

A. Data set identity

Title: ATLANTIC AMPHIBIAN TRAITS: a data set of morphological and ecological traits of amphibians in the Atlantic Forest

B. Data set identification code

Suggested data set identity codes:

ATLANTIC_AMPHIBIAN_TRAITS_individual.csv

ATLANTIC_AMPHIBIAN_TRAITS_species.csv

C. Data set description

1. Originators

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2. Abstract

The lack of knowledge about species' functional traits represents a major challenge given the increase in focus on functional diversity studies. Typically, available at the species-level, these data overlook individual variance within species. Amphibians are particularly suited for trait-based investigations due to their pivotal role connecting terrestrial and freshwater ecosystems through their biphasic life cycle. The Atlantic Forest of South America (AF) hosts approximately 720 species of amphibians, with over 70% being endemic. Despite their high and endemic diversity, the substantial loss of habitat and microhabitats in this hotspot threatens a significant portion of amphibian diversity. Thus, we present the ATLANTIC AMPHIBIAN TRAITS, a data set that includes morphological and ecological traits at both individual and species-level. At the individual-level, we measured 2,489 individuals representing 357 anuran species across 17 families (50% of amphibian diversity of AF), sourced from specimens in the CFBH collection. We assessed 12 continuous morphological traits, including body size (snout-vent length—SVL), head shape (width and length), and locomotor limbs (humerus, radioulna, hand, femur, tibiofibula, tarsus, foot, hindlimb, and forelimb), relevant to natural history characteristics, feeding, trophic levels, locomotion, migration, and dispersion. Additionally, we provide voucher collection numbers, complete taxonomy, geographic information, collection dates, and collector names for these individuals. The data set at species-level comprises 17 ecological traits (related to habitat, reproduction, and trophic characteristics) from 533 amphibian species across 21 families (74% of amphibian diversity of AF). These ecological traits, sourced from literature, comprise two continuous traits (female and male body size—SVL values), and 15 categorical traits covering various aspects such as locomotion mode, habitat preferences, reproductive modes, and toxicity levels. Acknowledging the data set's incompleteness given the vast amphibian diversity in the AF, we view this effort as a significant step in compiling individual amphibian traits for the

Neotropical region. This data set serves as a valuable resource for advancing research on anthropogenic and climate change impacts on amphibian functional diversity within the AF ecosystems.

D. Keywords

Tropical forest, Amphibia, Anura, Gymnophiona, Traits, Functional diversity, Individual variation.

E. Description

Class II. Research origin descriptors

A. Overall project description

1. Identity

A compilation of morphological and ecological traits at both individual and species levels for amphibians in the Atlantic Forest of South America.

2. Originators

The ATLANTIC AMPHIBIAN TRAITS project was coordinated by Maurício H. Vancine, Paula R. Anunciação, Kauã S. Duarte, Milton C. Ribeiro, and Célio F. B. Haddad at the Universidade Estadual Paulista (Unesp). This is part of ATLANTIC SERIES, which is led by Mauro Galetti and Milton Ribeiro, Universidade Estadual Paulista (Unesp), Brazil.

3. Period of study

The measurement data and literature data were taken and compiled between 2016 and 2017.

4. Objectives

The aim of this data paper was to provide morphological and ecological traits at both individual and species levels for amphibians across the entire Atlantic Forest of South America.

5. Abstract

Same as above.

6. Sources of funding

The compilation of this data set was supported by São Paulo Research Foundation (FAPESP) grants #2022/01899-6 (MVH) #2021/10639-5 (CFBH), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) grants fellowships (MVH), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) research fellowship (CFBH). PRA was supported by the Coordenação de Aperfeiçoamento de Pessoal de NívelSuperior – Brazil (CAPES) – Finance Code 001 and by Programa de Doutorado Sanduíche no Exterior (PDSE—#88881.134118/2016-01).

B. Specific subproject description

1. Site description

Atlantic Forest extends from 3º S to 33º S and from 35º W to 58º W with about 1.63 km^2, covering coastal and inland portions of Brazil, Argentina, and Paraguay (Marques et al. 2021) (Figure 1). Due to this large extension, the Atlantic Forest boundaries create important ecotones with other vegetation domains such as Cerrado, Caatinga, Chaco, and Pampa (Marques et al. 2021). Within the AF, the vegetation forms a complex mosaic composed of five forest vegetation types—Dense Ombrophilous, Open Ombrophilous, Mixed Ombrophilous, Semideciduous Seasonal, and Deciduous Seasonal (Joly et al. 2014). Additionally, the Atlantic Forest also includes mangroves and coastal scrub vegetation (Marques et al. 2021). Furthermore, there are many associated ecosystems such as altitude grasslands (*campos de altitude*), oceanic islands, beaches, rocky shores, dunes, marshes, inland swamps, and mountain forest (brejos de altitude) in the Northeast region (Scarano 2002).

2. Experimental or sampling design

None.

3. Research methods

Trait types and levels

Following the proposition of Functional Trait Group (FTG) for amphibians of Tsianou and Kallimanis (2016), Tsianou and Kallimanis (2019), Tsianou and Kallimanis (2020), and Vasconcelos et al. (2019), we select morphological and ecological (habitat-related, reproductive, and trophic) traits. We classified the traits in two levels: *individual-level*, when we took measurements from individuals; and *species-level*, when we gathered

information from literature (Haddad and Prado 2005, Haddad et al. 2013). The body size is linked to physiological and ecological traits, such as hunting tolerance, dispersal ability, predator-prey relationships, and sexual selection (Salgado-Negret et al. 2015, Campos et al. 2017, Lourenço-de-Moraes et al. 2020). The sizes of the fore and hind limbs are associated with locomotion, head shape influences species' feeding behaviors, locomotion mode correspond to different types of locomotion, and the presence of toe disc influences climbing ability in vegetation (Emerson 1988, Pough et al. 2015, Salgado-Negret et al. 2015). The activity, habitat preferences, and habit are related to habitat occupation and partitioning (Haddad and Prado 2005, Haddad et al. 2013, Salgado-Negret et al. 2015). The reproductive mode, calling site, oviposition, egg type, and tadpole nutrition are related to reproductive characteristics (Haddad and Prado 2005, Haddad et al. 2013, Salgado-Negret et al. 2015). Abundance and toxicity are trophic traits related to hunting tolerance and predator-prey and relationships (Salgado-Negret et al. 2015, Campos et al. 2017, Lourenço-de-Moraes et al. 2020). All morphological and ecological traits are detailed in Table 1.

Table 1. List of morphological and ecological (reproductive, habitat-related, and trophic) traits of amphibians in the ATLANTIC AMPHIBIAN TRAITS.

Functional trait group	Level	Trait	Type	Unit/category	Source
Morphological	Individual	Body size	Continuous	Millimeters	CFBH collection
Morphological	Individual	Head width	Continuous	Millimeters	CFBH collection
Morphological	Individual	Head length	Continuous	Millimeters	CFBH collection
Morphological	Individual	Humerus	Continuous	Millimeters	CFBH collection
Morphological	Individual	Radioulna	Continuous	Millimeters	CFBH collection
Morphological	Individual	Hand	Continuous	Millimeters	CFBH collection
Morphological	Individual	Femur	Continuous	Millimeters	CFBH collection
Morphological	Individual	Tibiofibula	Continuous	Millimeters	CFBH collection

Morphological	Individual	Tarsus	Continuous	Millimeters	CFBH collection
Morphological	Individual	Foot	Continuous	Millimeters	CFBH collection
Morphological	Individual	Forelimb	Continuous	Millimeters	CFBH collection
Morphological	Individual	Hindlimb	Continuous	Millimeters	CFBH collection
Morphological	Species	Male body size (SVL)	Continuous	Millimeters	Haddad et al. (2013)
Morphological	Species	Female body size (SVL)	Continuous	Millimeters	Haddad et al. (2013)
Morphological	Species	Male body size	Ordinal	Small, medium, large	Haddad et al. (2013)
Morphological	Species	Female body size	Ordinal	Small, medium, large	Haddad et al. (2013)
Morphological	Species	Toe disc	Binary	Presence, absence	Expert knowledge
Morphological	Species	Locomotion mode	Nominal	Hopper, hopper_burrower, jumper, swimmer, walker_hopper, walker_hopper_burrower, walker_jumper	Expert knowledge and Pough et al. (2015)
Habitat-related	Species	Activity	Nominal	Nocturnal, diurnal, nocturnal and diurnal	Haddad et al. (2013)
Habitat-related	Species	Adult habitat	Nominal	Forested areas, open areas, forested and open areas	Haddad et al. (2013)
Habitat-related	Species	Adult habit	Nominal	Aquatic, arboreal, cryptic, fossorial, phytotelmata, rheophilic, semiaquatic, terrestrial	Haddad et al. (2013)
Habitat-related	Species	Tadpole habit	Nominal	Terrestrial, running_water, still_water, froglet, no_tadpole	Haddad et al. (2013)
Reproductive	Species	Reproductive mode	Nominal	1 to 39 (each value represents a reproductive mode in Haddad & Prado (2005))	Haddad et al. (2013)
Reproductive	Species	Calling site	Nominal	Bamboo_grove, bromeliad, cave_burrow, forest_floor, low_vegetation,	Haddad et al. (2013)

				river_stream_ rivulet, rock_wall, swamp_or_pond, river_or_stream_backwaters, tree_crown, do_not_call	
Reproductive	Species	Oviposition	Nominal	Aerial_plant, basin, bubble_nest, carried_adult, chamber, directly_terrestrial, directly_water, foam_nest, subterranean_nest	Haddad et al. (2013)
Reproductive	Species	Egg type	Nominal	Aquatic, arboreal, terrestrial	Haddad et al. (2013)
Reproductive	Species	Tadpole nutrition	Nominal	Direct_development, endotrophic, exotrophic	Haddad et al. (2013)
Trophic	Species	Abundance	Ordinal	Rare, infrequent, frequent	Haddad et al. (2013)
Trophic	Species	Toxicity	Ordinal	Non_toxic, unpalatable_or_bad_odor, toxic	Haddad et al. (2013)

Individual-level traits

The *individual-level* traits were derived from measurements carried out on 2,489 individuals from 357 anuran species across 17 families (50% of amphibian diversity, following Figueiredo et al. (2021) and taxonomic update using FROST 6.2 (Frost, 2023)), as detailed in Table 2 and Table 3. These measurements were obtained from specimens in the Célio F.B. Haddad amphibian collection (CFBH, UNESP, Rio Claro, SP, Brazil) between 2016 and 2017. As of October 2020, the CFBH housed more than 45,000 amphibian specimens from 30 families and 111 genera, representing over 800 species, making it the third-largest amphibian collection in Brazil (Silva et al. 2021). These measurements were taken with a digital caliper Mitutoyo 150 mm Digimatic Caliper (precision 0.01 mm), on one to 20 adult males of each species, depending on availability in the collection. When male identification was not explicit in the database, they were identified by the presence of vocal sacs, nuptial pads, or hypertrophied forelimb musculature. Measurements of the fore and hind limbs were consistently taken on the right side of the individuals to facilitate and standardize the measurements with the individuals held using the left hand and the caliper operated with the right hand. Figure 2 shows some images of the measurement process.

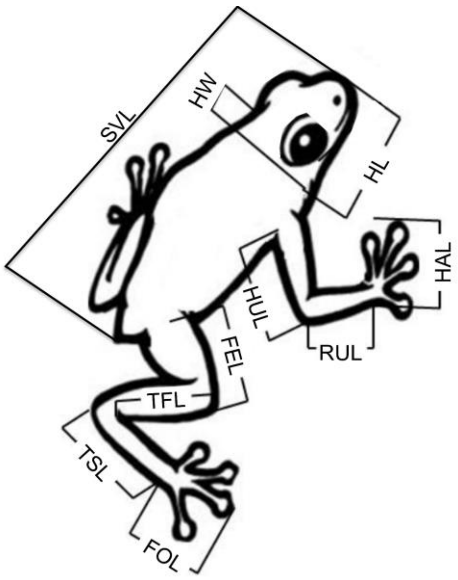
Figure 2. Images of the process of measuring morphological characteristics obtained from adult male anurans from the CFBH collection.

We carried out a detailed data check, analyzing the measurement variability for each species and removing any conflicting measurements, considering the possibility of errors in the measurements taken. Additionally, we assigned geographic coordinates based on measured specimens from the CFBH collection and obtained municipal coordinates (referred to as approximate coordinates) for locations lacking measured specimens (called approximate coordinates) using the R package *tidygeocoder* (Cambon et al. 2021). Based on these coordinates, we removed records that did not have an overlapping spatial distribution in the Atlantic Forest limit (Muylaert et al. 2018).

The individual measurements are as follows, in accordance with the guidelines outlined by Emerson (1988) and Watters et al. (2016). *Body size* was measured as snout–vent length (SVL) [direct line distance from tip of snout to posterior margin of vent]. *Head width* was measured as the distance between the jaw insertions. *Head length* was measured

from the posterior of the jaws to the tip of the snout. *Humerus* was measured as humerus length [distance from the humerus insertion to the elbow]. *Radioulna* was measured as radioulna length [from the flexed elbow to the base of the outer palmar tubercle]. *Hand* was measured as hand length [from the base of the outer palmar tubercle to the tip of Finger IV—the longest finger]; for some individuals, the hand is not possible to measure, so we incorporated this measurement in the *Radioulna*. *Femur* was measured as femur length [distance from the vent to the knee]. *Tibiafibula* was measured as tibiafibula length [distance from the outer surface of the flexed knee to the heel/tibiotarsal inflection]. *Tarsus* was measured as tarsus length [from the tibiotarsal articulation to the base of the inner metatarsal tubercle]. *Foot* was measured as foot length [from the base of the inner metatarsal tubercle to the tip of Toe IV—the longest toe]; for some individuals, the foot was not possible to measure, so we incorporated this measurement in the *Tarsus*. *Forelimb* was calculated as the sum of the humerus, radioulna, and hand lengths. *Hindlimb* was calculated as the sum of the femur, tibiafibula, tarsus, and foot lengths. Information regarding *Toe disc* presence and *Locomotion mode* was obtained and compiled based on expert knowledge.

Detailed descriptions and illustrations of the morphological trait measurements are provided in Figure 3.



Morphological traits
1. SVL = Snout–vent length
2. HW = Head width
3. HEL = Head length
4. HUL = Humerus length
5. RUL = Radioulna length
6. HAL = Hand length
7. FEL = Femur length
8. TFL = Tibiafibula length
9. TSL = Tarsus length
10. FOL = Foot length

Figure 3. Description and location morphological trait measurements for adult male anurans from the CFBH collection. Source: adapted from Corrêa Filho (2013).

The distribution of individual body size measurements (the most common measurement) from each family showed a congruent pattern (Figure 4): the families Bufonidae, Ceratophryidae, and Ranidae displayed the highest values for all morphological traits measured, indicating larger-sized individuals within these families. Bufonidae, Cycloramphidae, Odontophrynidae, and Ranidae showed greater dispersion among all families, with species showing great variability within these families. On the other hand, the families Brachycephalidae, Aromobatidae, and Strabomantidae presented the lowest values for forelimb, hindlimb and SVL.

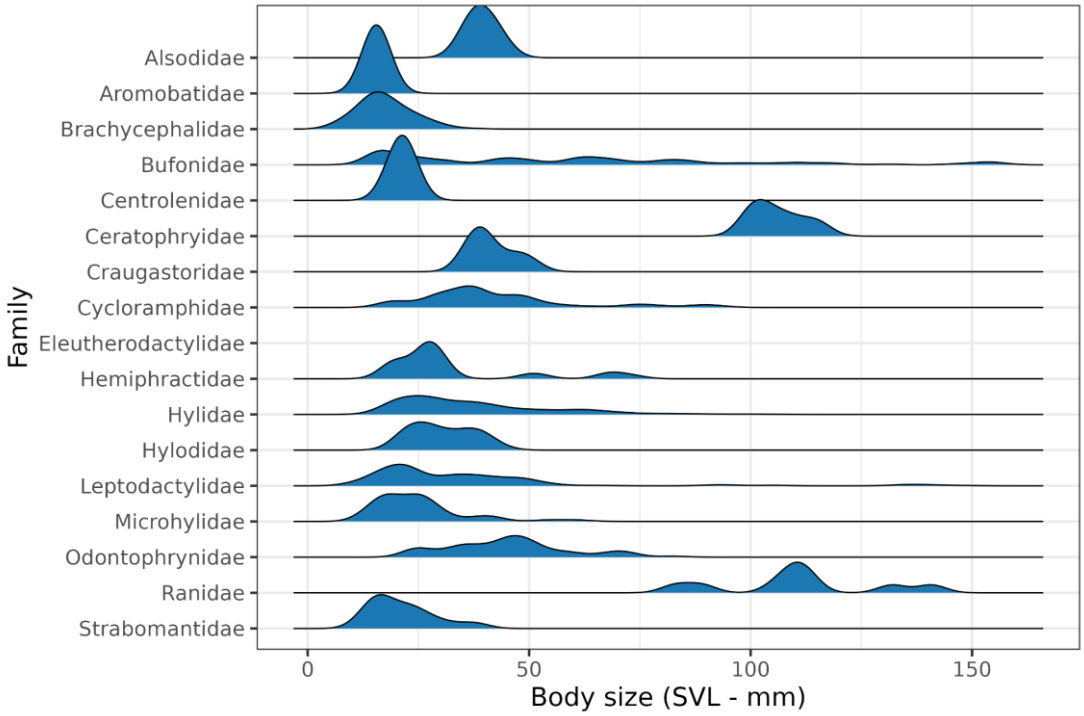


Figure 4. Variation in the body size (SVL; mm) of anurans at the individual level across families in the ATLANTIC AMPHIBIAN TRAITS data set.

The Hylidae and Leptodactylidae families had the largest number of species and individuals measured, as well as the most locations with measurements. These families are known for their greater diversity of amphibians in the Neotropical and Atlantic Forest regions (Duellman 1999, Haddad et al. 2013). Conversely, the families Craugastoridae, Aromobatidae, Alsodidae, Ranidae, Ceratophryidae, and Eleutherodactylidae each had only one species with a few individuals measured at a limited number of locations, making them the least diverse families in the biome (Duellman 1999, Haddad et al. 2013) (Table 2).

Table 2. Number of species, individuals, and locality (with coordinates) information per family of anuran measured in CFBH collection.

Family	Species	Individual	Locality
Alsodidae	1	10	3
Aromobatidae	1	10	4
Brachycephalidae	30	181	75
Bufonidae	16	128	80
Centrolenidae	2	20	17
Ceratophryidae	1	5	3
Craugastoridae	1	10	8
Cycloramphidae	15	93	35
Eleutherodactylidae	1	1	1
Hemiphractidae	5	25	16
Hylidae	168	1271	702
Hylodidae	18	103	61
Leptodactylidae	59	389	226
Microhylidae	16	112	48
Odontophrynidae	13	71	47
Ranidae	1	9	5
Strabomantidae	9	51	24
Total	357	2489	1355*

*Values are higher than those reported in the "Locality" column of the "ATLANTIC_AMPHIABIAN_TRAITS_individual.csv" file and Table 4. This discrepancy arises because we utilized geographic coordinate data to specify the locations accurately.

Species-level traits

The *species-level* traits were derived from several sources, including Haddad et al. (2013), Haddad and Prado (2005), Pough et al. (2015), and expert knowledge (CFB Haddad, unpublished data). The traits are documented for 533 amphibian species, two orders, and 21 families, which represent 74% of amphibian diversity (Table 3) (following Figueiredo et al. (2021) and taxonomic update using FROST 6.2 (Frost, 2023)). Our data collection included *morphological traits* such as two continuous (female and male body size—SVL values), three categorical (female and male body size—small, medium, large; and locomotion mode—hopper, hopper-burrower, jumper, swimmer, walker-hopper, walker-hopper-burrower, walker-jumper), and one binary (presence of toe disc—related to vegetation

climbing). We also gathered *habitat-related traits* such as activity patterns, adult habitat preferences, adult habits, and tadpole habits, which help in understanding species niche utilization and partitioning. Additionally, we compiled *reproductive traits* such as five categorical (reproductive mode, calling site, oviposition, egg type, and tadpole nutrition), all of which are crucial aspects of amphibian life history. We derived reproductive mode into four traits, following Haddad and Prado (2005): for each reproductive number, we separated into tadpole habit, tadpole nutrition, oviposition, and egg type. And finally, we documented trophic traits such as abundance and toxicity, which are significant in predator-prey relationships within ecosystems. We also provided information on the endemicity of species within the Atlantic Forest biome, offering valuable insights into conservation priorities for this region.

The species-trait information that was most complete included the presence of toe disc and locomotion mode, as we inferred these traits based on taxonomy (family and genus) using expert knowledge. Subsequently, the data that provided the most information for the species were male body size (SVL), male body size (categorical), adult habitat, and tadpole habit. These traits are generally more readily available, common, and easier to obtain for species, thus leading to their greater availability. In contrast, information on the activity period and female body size (SVL) were the least complete. This is due to the rarity of this information, stemming from challenges such as studying the activity periods or to find females in the field. Additionally, encounters and collections of females are relatively rare for most species, as they usually do not emit advertisement or aggressive calls (Wells, 2007), making them difficult to locate (Figure 5).

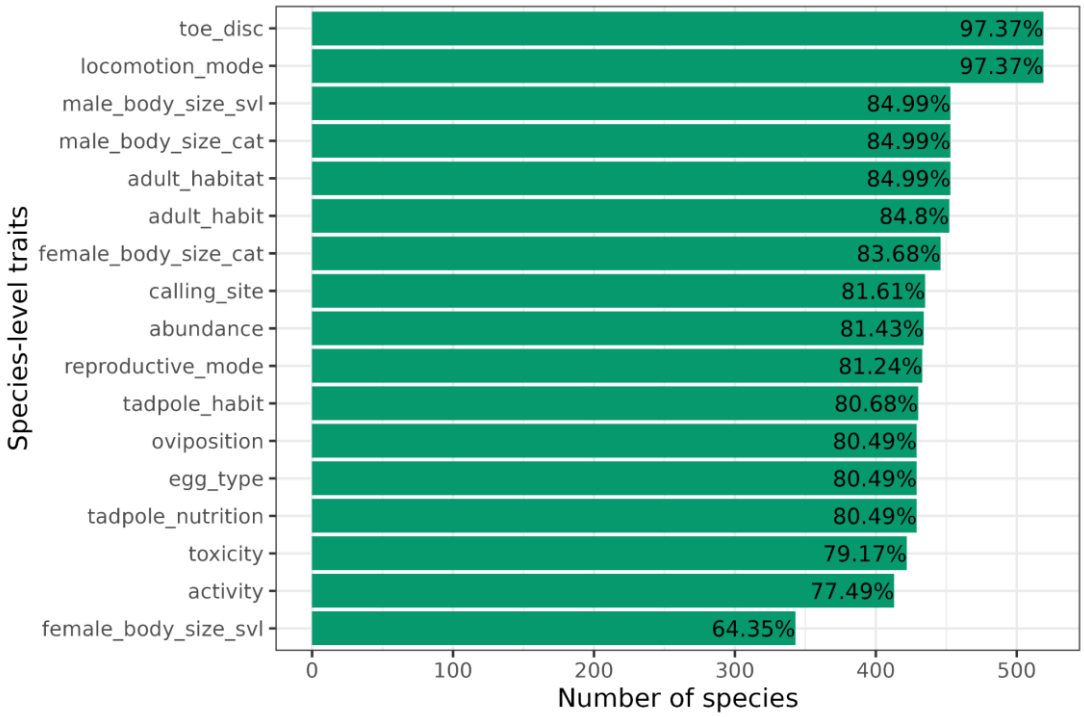


Figure 5. Number of species at species-level for the ecological traits in ATLANTIC AMPHIBIAN TRAITS. The percentage represents the number of species with trait information relative to the total number of species measured.

Regarding the level at which measurements were taken, as expected, there was more data collected at the species level (covering 74% of all species) than at the individual level (50% of the total species). Despite this, we managed to be included 17 of the 20 anuran families, accounting for 85% of all families in our data set. For the order Gymnophiona, there was more data gathered at the species level than the number of species listed by Figueiredo et al. (2021) (Table 3). The representation of species by families ranged from 0 to 100%, with an average representation of around 70% at the species level and 40% at the individual level for Anura. The families Hylidae and Leptodactylidae had the largest number of species with gathered data at the species level, reflecting their status as the most diverse families in the study region (Haddad et al. 2013). These families also showed a higher percentage of species represented at both species and individual levels (Table 3).

Table 3. Comparison between the number of amphibian species reported in the Atlantic Forest by Figueiredo et al. (2021) and the number recorded in this data set at both species and individual-level traits.

Order	Family	Number of species in the Atlantic Forest (Figueiredo et al. 2021)	Number of species at species-level traits	Percentage of number of species at species-level traits (%)	Number of species at individual-level traits	Percentage of number of species at individual-level traits (%)
Anura	Allophrynidae	1	0	0	0	0
Anura	Alsodidae	1	1	100	1	100
Anura	Aromobatidae	2	1	50	1	50
Anura	Brachycephalidae	71	49	69	30	42
Anura	Bufonidae	59	34	58	16	27
Anura	Centrolenidae	4	3	75	2	50
Anura	Ceratophryidae	4	2	50	1	25
Anura	Craugastoridae	3	3	100	1	33
Anura	Cycloramphidae	36	35	97	15	42
Anura	Dendrobatidae	2	0	0	0	0
Anura	Eleutherodactylidae	7	5	71	1	14
Anura	Hemiphractidae	16	13	81	5	31
Anura	Hylidae	271	210	77	168	62
Anura	Hylodidae	46	40	87	18	39
Anura	Leptodactylidae	107	66	62	59	55
Anura	Microhylidae	28	21	75	16	57
Anura	Odontophrynidae	32	22	69	13	41
Anura	Pipidae	1	1	100	0	0
Anura	Ranidae	2	2	100	1	50
Anura	Strabomantidae	14	11	79	9	64
Gymnophiona	Caeciliidae	1	1	100	0	0
Gymnophiona	Siphonopidae	8	8	100	0	0
Gymnophiona	Typhlonectidae	3	5	167	0	0
Total		719	533	74	357	50

Taxonomy and systematics

We follow the taxonomy proposed by FROST 6.2 in December 2023 (Frost, 2023) using the R package *AmphiNom* (Liedtke 2019).

Data limitations and potential enhancements

We recognize that this data set is still very incipient given the enormous diversity of amphibians, since the information gathered at individual level represents only 50% of the amphibian's species diversity in the AF. In contrast, information collected at species level is

more complete, covering 74% of the species in the AF. Other data papers focusing on birds (ATLANTIC BIRD TRAITS; Rodrigues et al. 2019) (80% of the species at individual-level) and mammals (ATLANTIC MAMMAL TRAITS, Gonçalves et al. (2018a)) (94% of the species at individual-level) have managed to compile much more information. This is because these groups are more extensively studied and have more available trait information (Gonçalves-Souza et al. 2023).

Taxonomic errors represent another limitation of this data set. Given that we measured nearly 2,500 individuals, it is possible that we made errors in identifying the specimens deposited or that the species were previously misidentified. The field of amphibian taxonomy is dynamic, undergoing continuous taxonomic reviews driven by new genetic, morphological, and ecological data (Guerra et al. 2020). We recognize the potential for misclassification or uncertainty in taxonomic assignments, particularly for species once believed to be widespread but now identified as cryptic complexes. While we have relied on expert identification, this limitation introduces a level of uncertainty into our data set. It is impractical to individually verify the taxonomic identity of each specimen due to the scale of our data set. Furthermore, we still have to recognize that our measurements may be subject to limitations, since we take measurements of preserved individuals, which may experience deformations over time due to fixation or storage (Hayek et al. 2001, Deichmann et al. 2009). However, we attempted to mitigate this issue by excluding measurements that deviated significantly from the species averages.

Data limitations related to sample size discrepancies and environmental variability in the data set can also impact the robustness and interpretability of the data. Variability in the number of individuals measured per species (sample size discrepancies) can introduce biases and affect the statistical power of potential analyses, particularly for less common species. Additionally, the Brazilian Atlantic Forest region exhibits diverse environmental conditions, including variations in microhabitats, climate, and ecological niches (Haddad et al. 2013; Vancine et al. 2023). This environmental variability can influence the expression of morphological traits and ecological behaviors among amphibian species, complicating data interpretation and generalization across different habitats within the region. Understanding these limitations is crucial for appropriately interpreting and contextualizing findings derived from the data set, highlighting the need for caution and detailed environmental metadata when analyzing amphibian traits in this biodiverse region.

The data set can be enhanced by incorporating data from taxonomic literature, which provides comprehensive descriptions of various morphological measurements.

Morphological characteristics serve as crucial taxonomic criteria and are extensively documented in taxonomic literature. These characteristics are often measured across multiple specimens, including both males and females, in addition to type specimens (Huang et al. 2023). They encompass a range of ecological functions, such as body size, characteristics of locomotor limbs, as well as measurements like eye diameter and tympanum size (Pough et al. 2015, Thomas et al. 2020).

Amphibians still have an aspect of functional diversity that remains relatively unexplored yet holds great potential: acoustic traits (De Mello Bezerra et al. 2021; Sugai et al. 2021a). Almost all anurans exhibit various types of vocalizations, being the primary mode of communication among adults (Duellman and Trueb 1994, Wells 2007). These vocalizations serve several ecological functions, primarily associated with life history processes such as sexual selection, reproduction, partner localization and recognition, as well as territorial behaviors (Duellman and Trueb 1994, Wells 2007). Acoustic information extends beyond mere communication and has significant applications in fields such as taxonomy, ecology, conservation, behavior, and passive acoustic monitoring studies (Köhler et al. 2017, Sugai et al. 2021a, 2021b, Cañas et al. 2023). Among the main vocalizations, the advertisement call stands out, being the most frequently emitted by male anurans (Duellman and Trueb 1994, Wells 2007, Emmrich et al. 2020). From these calls, several acoustic parameters can be obtained, such as call duration, call frequency, pulse frequency, and dominant frequency, which are crucial for species identification and differentiation (Köhler et al. 2017). Despite this, there is still a substantial knowledge gap persists concerning these traits, especially in Brazilian regions renowned for their biodiversity, such as the Atlantic Forest, and within highly diverse families like Hylidae and Leptodactylidae (Guerra et al. 2018). Although some studies have begun to fill these gaps, the available information remains limited compared to the potential wealth of data awaiting exploration (Röhr et al. 2016, Forti et al. 2019, Cañas et al. 2023).

An additional valuable source of data comes from sound libraries, which, like scientific collections, house recordings of diverse species (Dena et al. 2020). These recordings serve as a rich resource for extracting acoustic parameters. Notable examples include the Fonoteca Zoológica of the National Museum of Natural Sciences (https://www.fonozoo.com), the Macaulay Library of the Cornell Lab of Ornithology (https://www.macaulaylibrary.org), and the Fonoteca Neotropical Jacques Vielliard of the Campinas State University (https://www2.ib.unicamp. br/fnjv) (Guerra et al. 2018). Furthermore, it is essential to integrate these measurements into fieldwork protocols, which

is currently uncommon in this context (Salgado-Negret et al. 2015). Finally, implementing this same protocol in collections will ensure that these measurements are also accessible in online databases, such as GBIF (www.gbif.org) and SpeciesLink (specieslink.net), BIEN (bien.nceas.ucsb.edu/bien; Enquist et al. 2016) and R package *BIEN* (Maitner et al. 2018).

Class III. Data set status and accessibility

A. Status

1. Latest update

January 2024.

2. Latest archive date

January 2024.

3. Metadata status

Last updated January 2024, version submitted.

4. Data verification

None.

B. Accessibility

1. Storage location and medium

The original ATLANTIC AMPHIBIAN TRAITS data set can be accessed as supporting information for this Data Paper publication in Ecology. Updated versions and additional information are available on the Open Science Framework (OSF) (https://doi.org/10.17605/OSF.IO/Q8EGM) and code is accessible on GitHub (https://github.com/mauriciovancine/ATLANTIC-AMPHIBIAN-TRAITS).

2. Contact persons

Maurício Humberto Vancine (mauricio.vancine@gmail.com).

3. Copyright restrictions

None.

4. Proprietary restrictions

a. Release date

None.

b. Citation

When using the data from this Data Paper in publications or teaching events, please cite the paper using the appropriate citation format.

c. Disclaimer(s)

None.

5. Costs

None.

Class IV. Data structural descriptors

The data set contains two files: ATLANTIC_AMPHIBIAN_TRAITS_individual.csv and ATLANTIC_AMPHIBIAN_TRAITS_species.csv.

A. Data set file

1. Identity: ATLANTIC_AMPHIBIAN_TRAITS_individual.csv

2. Size: 35 columns and 2490 rows records, including header row, with a size file of 805 kB.

3. Format and storage mode: comma-separated values (.csv).

4. Header information: See column descriptions in section B.

5. Alphanumeric attributes: Mixed.

1. Identity: ATLANTIC_AMPHIBIAN_TRAITS_species.csv

2. Size: 27 columns and 534 rows records, including header row, with a size file of 127 kB.

3. Format and storage mode: comma-separated values (.csv).

4. Header information: See column descriptions in section B.

5. Alphanumeric attributes: Mixed.

B. Variable information

1) Table 4. **Information in the ATLANTIC AMPHIBIAN TRAITS data set for individuals**. Description of the fields related to the study site in the ATLANTIC_AMPHIBIAN_TRAITS_individual.csv.

Variables identify	Variable description	Levels	Example
id	Identification code for each measurement	0001-2489	0001
voucher	Voucher number of specimens in CFBH collection	2485	29856
species	Species name recorded in the measurement moment	361	*Aplastodiscus cavicola*
species_frost2023	Valid species name according to Frost (2023)	357	*Aplastodiscus cavicola*
order	Taxonomic order according to Frost (2023)	1	Anura
superfamily	Taxonomic superfamily according to Frost (2023)	2	NA
family	Taxonomic family according to Frost (2023)	17	Hylidae
subfamily	Taxonomic subfamily according to Frost (2023)	11	Hylinae
genus	Taxonomic genus according to Frost (2023)	57	Adelophryne
collection	Museum collection to which the specimen belongs	5	CFBH
body_size	Body size reported as snout–vent length (SVL) in millimeters	6.72-156.16	34.41
head_width	Distance between the jaw insertions in millimeters	2.64-67.56	11.7
head_length	Distance from the posterior of the jaws to the tip of the snout in millimeters	1.81-53.62	10.94
humerus	Humerus length in millimeters	1.46-30.72	5.56
radioulna	Radioulna length in millimeters	1.50-74.07	17.45
hand	Hand length in millimeters	1.08-38.39	NA
femur	Femur length in millimeters	3.30-73.70	17.92
tibiafibula	Tibiafibula length in millimeters	3.09-70.76	17.69
tarsus	Tarsus length in millimeters	2.28-110.03	24.95
foot	Foot length in millimeters	2.17-73.39	NA

forelimb	Sum of the humerus, radioulna, and hand in millimeters	4.36-101.44	23.01
hindlimb	Sum of the femur, tibiafibula, tarsus, and foot in millimeters	11.48-254.49	60.56
species_cfbh	Species name as reported in the CFBH collection	483	*Aplastodiscus cavicola*
country	Country name as reported in the CFBH collection	1	Brazil
state	State name code as reported in the CFBH collection	13	RJ
municipality	Municipality name as reported in the CFBH collection	309	Itatiaia
locality	Local name as reported in the CFBH collection	753	Pousada Chalés Terra Nova
longitude	Longitude in decimal degrees (WGS 84) as reported in the CFBH collection	255	NA
latitude	Latitude in decimal degrees (WGS 84) as reported in the CFBH collection	257	NA
longitude_approximate	Longitude approximates in decimal degrees (WGS 84)	311	-44.5633108
latitude_approximate	Latitude approximates in decimal degrees (WGS 84)	311	-22.4955278
colletion_date	Date of the record (yyyy-m-d) as reported in the CFBH collection	1044	2011-11-02
collector_name	Name of anuran collector as reported in the CFBH collection	617	C. Cassini & P. Taucce

2) Table 5. **Information in the ATLANTIC AMPHIBIAN TRAITS data set for species**. Description of the fields related to the study site in the ATLANTIC_AMPHIBIAN_TRAITS_species.csv.

Variables identify	Variable description	Levels	Example
id	Identification code assigned to each species	001-533	001
species_haddad2013	Species name as reported in Haddad et al. (2013)	533	*Limnomedusa macroglossa*
species_frost2023	Valid species name according to Frost (2023)	533	*Limnomedusa macroglossa*

order	Taxonomic order according to Frost (2023)	2	Anura
superfamily	Taxonomic superfamily according to Frost (2023)	2	NA
family	Taxonomic family according to Frost (2023)	21	Alsodidae
subfamily	Taxonomic subfamily according to Frost (2023)	12	Hylinae
genus	Taxonomic genus according to Frost (2023)	66	*Limnomedusa*
male_body_size_svl	Male body size reported as snout–vent length (SVL) in millimeters according to Haddad et al. (2013)	8.00-454.00	45.00
female_body_size_svl	Female body size reported as snout–vent length (SVL) in millimeters according to Haddad et al. (2013)	11.00-300.00	54.00
male_body_size_cat	Male body size according to Haddad et al. (2013): ● small: < 30 mm ● medium: 30-100 mm ● large: > 100 mm	small, medium, large	medium
female_body_size_cat	Female body size according to Haddad et al. (2013): ● small: < 30 mm ● medium: 30-100 mm ● large: > 100 mm	small, medium, large	medium
toe_disc	Toe disc presence according to expert knowledge: ● absent ● present	absent, present	absent
locomotion_mode	Locomotion mode according to expert knowledge and Pough et al. (2015): ● hopper ● hopper_burrower ● jumper ● swimmer ● walker_hopper ● walker_hopper_burrower ● walker_jumper	hopper, hopper_burrower, jumper, swimmer, walker_hopper, walker_hopper_ burrower, walker_jumper	hopper
activity	Activity according to Haddad et al. (2013): ● nocturnal: generally active during the night ● diurnal: generally active during the day	nocturnal, diurnal, nocturnal_and_diurnal	nocturnal

	● nocturnal and diurnal: generally active during both the night and day		
adult_habitat	Habitat according to Haddad et al. (2013): ● forested areas: plenty of trees or within forests ● open areas: no trees, including clearings in the forests, natural or man-made grasslands, rocky fields, swamps, and ponds outside the forests ● forested and open areas: both areas at the forest borders	forested_areas, open_areas, forested_and_open_areas	open areas, forested_areas
adult_habit	Habit according to Haddad et al. (2013): ● aquatic: found in aquatic environment, generally associated with aquatic vegetation ● arboreal: found on tree trunks and leaves of arboreal and herbaceous vegetation ● cryptic: hidden in galleries, crevices or in natural or excavated holes in the ground, ravines, or under the leaf litter ● fossorial: found in subterranean galleries generally excavated ● phytotelmata: found in water accumulated in plant structures ● rheophilic: found on rocks in streams or rivers ● semiaquatic: found in the interface between water and land ● terrestrial: found on the ground or in leaf litter on the forest floor	aquatic, arboreal, cryptic, fossorial, phytotelmata, rheophilic, semiaquatic, terrestrial	terrestrial
tadpole_habit	Tadpole habit according to Haddad & Prado (2005) and Haddad et al. (2013): ● terrestrial ● running_water ● still_water ● froglet ● no_tadpole	terrestrial, running_water, still_water, froglet, no_tadpole	still_water

reproductive_mode	Reproductive mode according to Haddad & Prado (2005) and Haddad et al. (2013)	1 to 37, oviparous, direct_development, viviparous	1
calling_site	Calling site according to Haddad et al. (2013): ● bamboo_grove ● bromeliad ● cave_burrow ● forest_floor ● low_vegetation ● river_stream_rivulet ● rock_wall ● stream_rivulet ● swamp_or_pond ● river_or_stream_backwaters ● tree_crown ● do_not_call	bamboo_grove, bromeliad, cave_burrow, forest_floor, low_vegetation, river_stream_rivulet, rock_wall, stream_rivulet, swamp_or_pond, river_or_stream_backwaters, tree_crown, do_not_call	river_stream_rivulet
oviposition	Oviposition according to Haddad & Prado (2005) and Haddad et al. (2013): ● aerial_plant ● basin ● bubble_nest ● carried_adult ● chamber ● directly_terrestrial ● directly_water ● foam_nest ● subterranean_nest	aerial_plant, basin, bubble_nest, carried_adult, chamber, directly_terrestrial, directly_water, foam_nest, subterranean_nest	directly_water
egg_type	Egg type according to Haddad & Prado (2005) and Haddad et al. (2013): ● aquatic ● arboreal ● terrestrial	aquatic, arboreal, terrestrial	aquatic
tadpole_nutrition	Tadpole nutrition according to Haddad & Prado (2005) and Haddad et al. (2013): ● direct_development ● endotrophic ● exotrophic	direct_development, endotrophic, exotrophic	exotrophic
abundance	Abundance according to Haddad et al. (2013): ● rare: species that are very hard to find in the field ● infrequent: species that are not very common and hard to find in the field ● frequent: species that are easy to find in the field with large populations	rare, infrequent, frequent	frequent

toxicity	Toxicity according to Haddad et al. (2013): ● toxic ● unpalatable_or_bad_odor ● non-toxic	toxic, unpalatable_or_bad_odor, non-toxic	NA
endemic_of_atlantic_forest	Endemic of Atlantic Forest according to Haddad et al. (2013): ● not_endemic ● endemic	not_endemic, endemic	not_endemic

C. Data anomalies

If no information is available for a given cell, this is indicated by "NA".

Class V. Supplemental descriptors

F. Publications and results

Part of this data set was used in the following publications: Campos et al. (2017), Campos et al. (2019), Lourenço-de-Moraes et al. (2020), Anunciação et al. (2023), Fontana et al. (2023) and Vancine et al. (*in prep.*).

G. History of data set usage

1. Data request history

None.

2. Data set updates history

None.

3. Review history

None.

4. Question and comments from secondary users

None.

CRediT authorship contribution statement

MHV: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing— original draft, Writing—review and editing. **PRA**: Conceptualization, Data curation, Investigation, Methodology, Writing—review and editing. **KSD**: Conceptualization, Data curation, Writing—review and editing. **DBD**: Conceptualization, Data curation, Writing—review and editing. **NA**: Data curation, Writing—review and editing. **LGND**: Data curation, Writing—review and editing. **RSCA**: Data curation, Writing—review and editing. **MCR**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing—review and editing. **CFBH**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing—original draft, Writing—review and editing.

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CONCLUSÃO

Esta tese buscou responder a duas questões principais: (1) como ocorreu a dinâmica espaço-temporal da estrutura da paisagem de todo o bioma da Mata Atlântica, e (2) como estrutura da paisagem afeta as dimensões da diversidade taxonômica e funcional de comunidades de anuros neste mesmo bioma. Nossos resultados trouxeram uma gama de novas perspectivas e entendimento para ações de conservação tanto para a Mata Atlântica como um todo, como para os anfíbios. Além disso, com a reunião e disponibilização dos dados geoespaciais e de atributos funcionais de anfíbios, os resultados ainda podem ser utilizados para outros estudos que busquem entender novos questionamentos acerca de como a estrutura da paisagem e a diversidade de anuros ocorrem na Mata Atlântica. Resumindo, nossos resultados demonstraram que:

- Nos últimos 34 anos, houve uma perda considerável de vegetação na Mata Atlântica até meados de 2005. Depois desta data, a vegetação se estabilizou, com recuperação de cerca de 1 Mha de vegetação florestal (0,6%) e aumento no número de fragmentos, em parte devido a políticas ambientais. Contudo, a Mata Atlântica ainda é um domínio altamente fragmentado: 97% dos fragmentos de vegetação são pequenos (<50 ha), com tamanho médio de fragmento entre 16,3 e 25,5 ha; 50-60% da vegetação está a <90 m de suas bordas, e o isolamento entre os fragmentos é alto (250-830 m). As áreas protegidas e territórios indígenas cobrem apenas 10% da vegetação da Mata Atlântica, e a maioria da vegetação se estende por mais de 10 km nessas áreas. Esses resultados possuem várias implicações para a manutenção dos processos de regeneração da vegetação da Mata Atlântica e toda sua biodiversidade, tendo em vista os impactos iminentes das mudanças climáticas e da expansão urbana e agropecuária nessa região.

- Atrelado aos resultados anteriores, disponibilizamos um conjunto de dados de informações geoespaciais integradas e em escala precisa (resolução = 30 m) para toda a extensão da Mata Atlântica para o ano de 2020. Esse conjunto de dados é composto por 500 rasters com métricas de paisagem, topografia, hidrografia e antrópicas. Esse conjunto de dados pode ser utilizado em novos estudos sobre a conservação da biodiversidade, como modelos de distribuição de espécies,

planejamento sistemático da conservação, regeneração e restauração florestal, auxiliando pesquisadores e a sociedade em geral na preservação da Mata Atlântica.

- Avaliamos o efeito da estrutura da paisagem (perda, fragmentação e desconexão de habitat) sobre a diversidade taxonômica e funcional de anuros na Mata Atlântica brasileira. Analisamos 324 comunidades abrangendo 274 espécies de anuros e 12 características funcionais para avaliar os índices de diversidade das comunidades de anuros. Nossos resultados indicaram que a perda de habitat foi o principal preditor tanto da diversidade taxonômica, quanto da diversidade funcional, embora a desconexão de habitat tenha sido a mais importante para pelo menos um componente da diversidade funcional. Esses resultados mostraram que a quantidade e a conectividade dos habitats florestais e aquáticos são essenciais para a manutenção de vários aspectos da diversidade de anuros na Mata Atlântica, principalmente relacionados à movimentação e uso do habitat. Concluímos que a conservação dos remanescentes florestais e sua conectividade com ambientais aquáticos como riachos e lagos, representadas por áreas de preservação permanentes como matas ciliares, são fundamentais para garantir os funcionamentos dos ecossistemas terrestres e aquáticos, assim garantindo os processos ecológicos inerentes a ambos, visto que os anuros necessitam da integridade de ambos, pois usam esses dois habitats durante seu ciclo de vida.

- Atrelado aos resultados anteriores, disponibilizamos um segundo conjunto de dados que inclui atributos morfológicos e ecológicos ao nível individual e de espécie de anfíbios na Mata Atlântica. Ao nível individual, há 12 medidas morfológicas de 2.489 indivíduos de 357 espécies de anuros em 17 famílias. Ao nível de espécie há 17 atributos ecológicas de 533 espécies de anfíbios em 21 famílias. Este conjunto de dados pode auxiliar no desenvolvimento de novas pesquisas sobre as influências antropogênicas e das mudanças climáticas no componente da diversidade funcional dos anfíbios na Mata Atlântica.