



LUCAS DEZIDERIO SANTANA

**CAPÕES NATURAIS DE FLORESTAS NEBULARES: EFEITO
DE BORDA E DIVERSIDADE FUNCIONAL**

**LAVRAS - MG
2021**

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DIVERSIDADE FUNCIONAL**

Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ciências Florestais, para obtenção do título de Doutor.

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Orientador

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LUCAS DEZIDERIO SANTANA

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DIVERSIDADE FUNCIONAL**

**NATURAL PATCHES OF CLOUD FOREST: EDGE EFFECT AND FUNCTIONAL
DIVERSITY**

Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ciências Florestais, para obtenção do título de Doutor.

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2021**

Aos meus pais, Bebel e Nilton, pelo exemplo de vida e amor e por entenderem todos os momentos de ausência nos últimos anos.

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Dedico

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*“Dou respeito às coisas desimportantes
e aos seres desimportantes.
Prezo insetos mais que aviões.
Prezo a velocidade
das tartarugas mais que a dos mísseis.
Tenho em mim esse atraso de nascença.
Eu fui aparelhado
para gostar de passarinhos.
Tenho abundância de ser feliz por isso.
Meu quintal é maior do que o mundo.”*

Manoel de Barros

RESUMO GERAL

As manchas florestais com bordas naturais (ex.: capões de mata) são áreas formadas naturalmente em meio a uma matriz campestre, possuindo diversos tamanhos e formatos e com transição abrupta para a vegetação circundante. Apesar de serem encontradas em várias regiões montanhosas tropicais pouco se sabe sobre a estruturação destes ecossistemas. Porém, podem produzir importantes modelos de estudo para compreensão de várias questões ecológicas, principalmente como o efeito de borda molda as comunidades de plantas, independentemente da perda de habitat. Nesse sentido, em dois artigos da presente tese buscou-se explorar os principais padrões estruturantes e funcionais destas áreas. A interpretação dos artigos está fundamentada em um conjunto de dados de 5495 indivíduos arbóreos de dez manchas de floresta nebulosa circundadas por campos de altitude do sudeste do Brasil. Em cada mancha foram estabelecidas cinco parcelas na borda e cinco no interior florestal. No primeiro artigo foi explorado como a borda e o interior florestal diferem nas características de solo, estrutura e métricas de diversidade, e até que ponto essas diferenças estão relacionadas ao tamanho e forma dos capões. Nesse sentido, mostramos que os habitats de borda e interior são altamente contrastantes para maioria dos atributos da comunidade avaliados. E muitas dessas diferenças foram semelhantes ou até mais severas do que as encontradas para fragmentos florestais de origem antrópica recém-criados. Além disso, verificamos que a forma e o tamanho das manchas são importantes direcionadores da estrutura e diversidade arbórea e que manchas com tamanhos menores e com formas irregulares apresentam maior efeito de borda. Já no segundo artigo foi avaliado se as bordas naturais apresentam traços e diversidade funcional distintos do interior florestal e como a inclusão da variação intraespecífica de traços funcionais pode influenciar a interpretação de padrões ecológicos existentes nestes habitats. Assim sendo, foi possível verificar que a borda e o interior apresentam indivíduos com traços funcionais distintos, porém, que amenizam o estresse inerente de cada habitat. A borda também se mostrou um habitat mais seletivo em termos de abrangência de traços funcionais, o que refletiu na menor diversidade funcional. Por fim, mostramos que as diferenças estatisticamente significativas entre os habitats, em relação aos traços e diversidade funcional, foram melhor observadas com a inclusão da variação intraespecífica, portanto, negligenciar esta variação nos estudos de diversidade funcional pode resultar em interpretações equivocadas sobre os padrões ecológicos.

Palavras-chave: borda natural, ecótono, fragmentação *per se*, gradiente borda-interior, tamanho e forma de manchas florestais, traços funcionais, variação intraespecífica.

GENERAL ABSTRACT

Forest patches with natural edges (e.g.: *capões de mata*) are areas formed naturally in the middle of the grassland matrix, having different sizes and shapes and with an abrupt transition to the open vegetation. Despite being found in several tropical mountainous regions, little is known about the structure of these ecosystems. However, they can produce important study models for understanding various ecological issues, especially how the edge effect shapes plant communities, regardless of habitat loss. Thus, in two articles of the present thesis, we sought to explore the main structural and functional patterns of these areas. The interpretation of articles is based on a data set of 5495 trees from ten cloud forest patches surrounded by highland grasslands in southeastern Brazil. In each patch, we established five plots right on the edge and five randomly distributed over the forest interior. In the first article we explored how forest edges and interiors differ in soil characteristics, structure and diversity metrics and the extent to which these differences are related to forest size and shape. In this sense, we show that the edge and interior are contrasting habitats for most of the evaluated community attributes. And many of those differences were similar or even harsher than the ones found for recently created anthropogenic forest fragment. In addition, we found that the shape and size patches are important drivers of tree structure and diversity and that patches with smaller sizes and irregular shapes have a greater edge effect. In the second article, we evaluated how forest edges and interiors differ in traits and functional diversity and how the inclusion of intraspecific variation of functional traits can influence the assessment of ecological patterns existing in those habitats. Therefore, we showed that the edge and interior have individuals with distinct functional traits, however, that alleviate the inherent stress of each habitat. The edge was also proved to be a more selective habitat in terms of range of functional traits, which reflected in less functional diversity. Finally, we show that the statistically significant differences between habitats, in relation to traits and functional diversity, were better observed with the inclusion of intraspecific variation, therefore, neglecting this variation in functional diversity studies can result in misinterpretations about ecological patterns.

Keywords: ecotone, edge-interior gradient, fragmentation *per se*, intraspecific variation, natural edge, plant functional traits, size and shape of forest patches

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PRIMEIRA PARTE

1. INTRODUÇÃO GERAL

As montanhas tropicais abrigam uma grande diversidade florística distribuída em formações vegetais campestres, arbustivas e florestais. Um fator importante para a diversidade de plantas nas montanhas tropicais é a heterogeneidade de ambientes encontrados nessas regiões o que pode levar a uma grande diferenciação da composição de espécies entre habitats de uma mesma região. As manchas florestais naturais (ex.: capões de mata), muitas das vezes inseridas nestes locais, são ilhas florestais imersas em uma matriz campestre com formato e tamanho diversos, contudo, com processos ecológicos ainda pouco conhecidos. Desta forma, representam importantes ecossistemas demandantes por estudos científicos.

Os capões ocorrem em áreas onde vegetação campestre e florestal coexistem. Na região tropical podem ser observadas em diferentes cadeias montanhosas, porém, no Brasil são mais comuns em altitudes superiores a 1.000 m.s.m. O Departamento de Botânica da Universidade Federal de Juiz de Fora (UFJF) vem estudando esses capões, especialmente na Serra da Mantiqueira, mais precisamente os capões do Parque Estadual da Serra do Papagaio (PESP) – Minas Gerais, Brasil. Estes estudos foram iniciados em meados do ano de 2010, com expedições de campo para conhecimento da flora local, pois até a presente data nenhum estudo florístico tinha sido realizado na região. Desde então várias expedições foram realizadas e de forma concomitante foram desenvolvidos trabalhos de cunho taxonômico e ecológico. Porém, os estudos eram voltados principalmente para flora herbácea-arbustiva e epifítica, além disso, tinham majoritariamente caráter qualitativo.

Com o intuito de expandir o conhecimento sobre a flora da região e particularmente sobre a flora arbórea dos capões de altitude, dois projetos científicos em órgãos de fomento à pesquisa entre os anos de 2014 e 2015 foram aprovados pelo grupo de estudo do Laboratório de Ecologia Vegetal da UFJF. O primeiro foi aprovado no edital universal do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq - 454008/2014-7) e o segundo na Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG - APQ 2165/14), ambos coordenados pelo professor Dr. Fabrício Alvim Carvalho. Os dois projetos visavam de forma pioneira caracterizar e acompanhar através de parcelas permanentes a estrutura e diversidade da vegetação arbustiva-arbórea dos capões de mata, contribuindo tanto para conservação da flora da região quanto para sanar uma importante lacuna no conhecimento ecológico desse ecossistema. Além disso, buscavam correlacionar os principais parâmetros

estruturais com variáveis físicas e químicas do solo, visando elucidar padrões de distribuição da vegetação relacionados aos gradientes ambientais.

Através dos projetos foi possível subsidiar trabalhos de iniciação científica, mestrado e doutorado. Dentre estes estudos merece destaque a tese intitulada “Capões de floresta nebulosa no Parque Estadual da Serra do Papagaio, Minas Gerais: composição, estrutura e heterogeneidade ambiental” (RIBEIRO, 2018), pois parte dos dados coletados serviram de base para o presente estudo. Com este trabalho constatou-se uma relativa heterogeneidade ambiental entre os capões. Porém, diferente do esperado, a variação encontrada não refletiu na comunidade arbórea, pois os capões apresentaram composição florística e estrutura relativamente homogêneas, fato esse que foi explicado pela pequena distância entre as manchas. Além disso, verificou-se que os capões de floresta nebulosa apresentam grande importância para a conservação da biodiversidade, por abrigarem importantes populações de espécies ameaçadas de extinção.

Com os diversos trabalhos e expedições de campo sendo desenvolvidos, a transição abrupta entre os habitats campestre (campos de altitude) e florestal (capões de mata) era algo que sempre chamava atenção dos colaboradores do projeto. Desta forma, diante da falta de conhecimento sobre este ambiente e de uma importante lacuna a ser preenchida para entendimento da formação e funcionalidade de manchas florestais, surgiu a inspiração de estudar as bordas dos capões. Levando em consideração que os capões apresentam bordas naturais e que os conhecimentos sobre bordas, em geral, são oriundos de fragmentos com perda de habitat, trabalhos nestes ambientes também podem servir de modelo para entendermos o efeito de borda sem o viés antrópico.

Com a aprovação no doutorado em 2016 do autor do presente trabalho na Universidade Federal de Lavras (UFLA) e ingresso no Laboratório de Ecologia Vegetal da mesma instituição, o intuito de estudar as bordas dos capões ganhou mais força. Isso aconteceu devido o conhecimento sólido formado ao longo dos últimos anos por este grupo ao trabalhar com bordas naturais de florestas de galeria em áreas de cerrado. Estas áreas estão sendo estudadas desde meados de 2008 quando foi aprovado o financiamento do projeto “Estrutura e dinâmica do componente arbustivo-arbóreo de bordas naturais em Matas de Galeria no Alto Rio Grande – MG” através do CNPq (478086/2008-3). O principal objetivo do projeto foi avaliar a estrutura e a dinâmica da vegetação lenhosa das bordas naturais de matas de galeria, de forma a compreender o seu funcionamento e interação com a vegetação do interior da floresta e com a vegetação não florestal circundante. Desde então outros projetos foram aprovados, sendo um

no CNPq (481842/2012-8) e outro na FAPEMIG (CRA - PPM-00374-13) e, com isso, várias pesquisas nos diferentes âmbitos da graduação e pós-graduação foram realizadas para tentar compreender quais os principais padrões e processos que regulam estes ambientes, todos coordenados pelo professor Dr. Eduardo van den Berg.

Os principais achados destes projetos mostram que as bordas naturais são ambientes altamente dinâmicos, com taxas de recrutamento maior que a mortalidade, indicando expansão das florestas para o campo. Contudo, fogo e clima em conjunto parecem ser os principais reguladores da dinâmica destas transições, mantendo um equilíbrio entre expansão e retração da floresta. Além disso, através dos estudos de grupos funcionais verificou-se que a floresta expande para os campos com as espécies pioneiras sendo as primeiras colonizadoras, seguidas das exigentes de luz e tolerantes à sombra. A distância da borda também mostrou forte influência na sobrevivência e crescimento das diferentes espécies, ou seja, espécies pioneiras tem maior sobrevivência e crescimento nas bordas, enquanto para os outros grupos funcionais os mesmos parâmetros aumentam em direção ao interior. Estes resultados evidenciam o quanto o fator borda pode ser um forte direcionador para o estabelecimento das espécies.

Diante da parceria estabelecida e orientação do professor responsável pelo presente laboratório, culminou no projeto desta tese com o objetivo central de avaliar a estrutura lenhosa e as variáveis edáficas de bordas naturais em manchas de florestas nebulares com matriz de campo de altitude. Além disso, entender como o efeito de borda atua na estruturação de habitats de borda e interior florestal e se o tamanho e forma das manchas exercem alguma influência nesta estruturação. Diante da falta de conhecimento sobre o funcionamento destas comunidades, buscamos ainda compreender se o fator borda atua como direcionador para alterações nos traços e na diversidade funcional da comunidade arbórea. E por fim, avaliar a importância da inclusão da variação intraespecífica dos traços em estudos de diversidade funcional.

2. REFERENCIAL TEÓRICO

2.1. Ambientes montanhosos

As regiões montanhosas são áreas com imprescindível riqueza de espécies. Devido à ampla variação topográfica em pequena escala, as montanhas apresentam diversos tipos de ambientes e formações vegetacionais (BERTUZZO et al., 2016; IRL et al., 2015;

MARTINELLI, 2007). Segundo algumas estimativas, os ambientes montanhosos são responsáveis por abrigar um quarto de toda biodiversidade terrestre, além de concentrar metade dos *hotspots* mundiais de biodiversidade (SPEHN et al., 2005).

Os serviços ecossistêmicos prestados por estas áreas são vários (EGAN; PRICE, 2017; LYNCH; MAGGIO, 2000). As montanhas desempenham um papel fundamental no ciclo da água, com relação direta com o clima regional; a vegetação e o solo dessas áreas desempenham papel fundamental na redução de riscos naturais; atuam como refúgios vegetacionais, principalmente em períodos extremos de mudanças climáticas; são importantes áreas para o estoque de carbono, além disso, possuem também valores espirituais e estéticos intrínsecos (CATALAN; NINOT; ANIZ, 2017; SPEHN et al., 2005; SPEHN; RUDMANN-MAURER; KÖRNER, 2010).

Globalmente, o relevo pouco propício à ocupação econômica e urbana levou a uma menor degradação de ecossistemas naturais montanhosos quando comparadas a áreas mais planas. No entanto, com o aumento da população mundial e consequente expansão agrícola, estes ambientes vêm sofrendo uma ampla degradação ambiental (EGAN; PRICE, 2017; SPEHN et al., 2005). Desmatamento, degradação de terras, desertificação, conversão de áreas nativas para cultivo de monoculturas e mineração são alguns dos sérios problemas que vem ocorrendo nesses ecossistemas (CATALAN; NINOT; ANIZ, 2017; KOHLER; WEHRLI; JUREK, 2014). Além disso, estudos recentes apontam que com o acelerado aumento da temperatura global, as montanhas estão entre as regiões mais sensíveis e ameaçadas com relação as mudanças climáticas. São esperadas mudanças drásticas na distribuição e mesmo extinção de espécies, retração de geleiras e alterações no ciclo hidrológico (NOGUÉS-BRAVO et al., 2007; THUILLER et al., 2005).

Dentre as regiões montanhosas, os maiores centros de diversidade de plantas estão nas montanhas tropicais, onde as condições climáticas adequadas e os altos níveis de geodiversidade proporcionam uma elevada riqueza de espécies (BARTHLOTT et al., 2005; KREFT; JETZ, 2007). Estas regiões abrangem uma área de apenas 0,2% da superfície terrestre, porém, abrigam cerca de 18.500 espécies de plantas endêmicas, o que corresponde a 6,2 % de todas as espécies de plantas vasculares (BARTHLOTT et al., 2005).

Na porção leste do Brasil, encontram-se as mais altas cadeias montanhosas da região oriental do continente sul-americano, com destaque para as Serras do Mar e da Mantiqueira. Admite-se que essas serras são provenientes de ciclos orogênicos, onde por dobramentos do escudo cristalino brasileiro e posteriormente processos de falhamentos, elevando o terreno

local, estas áreas tenham se formado (ALMEIDA; CARNEIRO, 1998; SARTORI; SARTORI, 2004). A Serra da Mantiqueira, onde foi realizado o presente estudo, é considerada como de importância biológica especial, devido à elevada riqueza de espécies da fauna e flora e ao alto grau de endemismo (COSTA; HERMANN, 2006).

2.2. Florestas nebulares

No complexo da Serra da Mantiqueira pode ser encontrada uma das formações vegetacionais características das montanhas tropicais, as Florestas Nebulares (FN) (POMPEU et al., 2018). Embora não estejam relacionadas com uma altitude definida, as FN são comumente observadas a partir de 1000 m acima do nível do mar (FAHEY; SHERMAN; TANNER, 2016) e podem ser definidas como florestas que frequentemente são encobertas por nuvens ou nevoeiros formados em geral ao nível do solo (BRUIJNZEEL; SCATENA.; HAMILTON, 2010; BUBB et al., 2004; FAHEY; SHERMAN; TANNER, 2016).

Além das chuvas, a ocorrência frequente de neblina proporciona entrada adicional de umidade para estes locais, por meio da condensação de água na superfície das plantas, em um processo denominado precipitação horizontal (BRUIJNZEEL; SCATENA.; HAMILTON, 2010; FAHEY; SHERMAN; TANNER, 2016). Inclusive, diante dessas condições climáticas específicas, alguns estudos têm demonstrado a forte adaptação de algumas espécies vegetais, típicas destas regiões, em absorver água através da superfície foliar e conduzir até as raízes (ELLER; LIMA; OLIVEIRA, 2013).

As FN estão distribuídas ao longo de toda região tropical, condicionadas por complexas interações entre o clima, relevo e circulação atmosférica. Entre as florestas montanhosas, as FN são consideradas *hotspots* de diversidade, não necessariamente em número absoluto de espécies, mas sim com relação ao número de espécies endêmicas e ameaçadas de extinção (BRUIJNZEEL; SCATENA.; HAMILTON, 2010; SPEHN; RUDMANN-MAURER; KÖRNER, 2010). A frequente presença de névoa encobrindo a vegetação, temperaturas mais baixas e maior concentração de ventos são condicionantes que acabam limitando a sobrevivência de algumas espécies nestas áreas, em contrapartida, propiciando uma flora peculiar para estas regiões (BRUIJNZEEL et al., 2010; WILLIAMS-LINERA; TOLEDO-GARIBALDI; HERNÁNDEZ, 2013). Corroborando essa ideia, em uma escala regional, Bertonecello et al. (2011) recentemente comprovaram que as FN compreendem uma formação fitogeográfica distinta das outras formações florestais na região Sul e Sudeste do Brasil.

Apesar dos serviços ecossistêmicos prestados pelas FN, como aporte hídrico, manutenção da biodiversidade e regulação do clima (BUBB et al., 2004; MARTÍNEZ et al., 2009; SPRACKLEN; RIGHELATO, 2014), estes ambientes são considerados um dos mais ameaçados do mundo (ALDRICH et al., 1997). Além das ameaças também enfrentadas pelas demais florestas tropicais, como conversão da paisagem em áreas agrícolas e de pastagem, incêndios florestais, exploração madeireira, mineração e introdução de espécies exóticas invasoras (BUBB et al., 2004), as FN são especialmente vulneráveis as mudanças climáticas (BRUIJNZEEL et al., 2010; BUBB et al., 2004; CATALAN; NINOT; ANIZ, 2017; MARTIN; BELLINGHAM, 2016).

Com o aumento da temperatura global, uma das respostas imediatas das espécies seria o deslocamento para áreas de maiores altitudes, de forma a manter as condições termais originais (TELWALA et al., 2013; WILSON et al., 2005). No entanto, para muitas espécies vegetais endêmicas de áreas nebulares, este ajuste via deslocamento espacial torna-se limitado devido a fatores edáficos (ANTUNES, dados não publicados) e uma vez que essas já estão “ilhadas” nos pontos de maior elevação altitudinal (SILVA et al., 2017). Além disso, outro fator ao qual as áreas com FN estão susceptíveis é a redução da nebulosidade em altitudes mais baixas, resultando em menor imersão das nuvens na floresta e conseqüente redução na captação de água pela vegetação (BUBB et al., 2004). Diante das ameaças enfrentadas pelas FN, estudos ecológicos nestas áreas ganham prioridade.

2.3. Fragmentação *per se* e os capões de mata

A fragmentação é geralmente considerada como um dos principais impulsionadores de mudanças negativas na biodiversidade dos ecossistemas terrestres e, portanto, amplamente vista como um aspecto de degradação do habitat (FARDILA et al., 2017; NEWBOLD et al., 2015). Com o aumento mundial de paisagens fragmentadas devido as atividades antropogênicas, surgiu uma demanda científica para tentar entender os mecanismos responsáveis pelos padrões e processos que regem a diversidade biológica nestas áreas (FAHRIG, 2003; FARDILA et al., 2017; HADDAD et al., 2015; PARDINI; NICHOLS; PÜTTKER, 2017; ROCHA-SANTOS et al., 2017; ROGAN; LACHER, 2018; WILSON et al., 2016). Porém, estes estudos estão altamente relacionados à perda de habitat (FAHRIG, 2017; HADDAD et al., 2015).

E para entendermos os mecanismos que governam a fragmentação, precisamos também compreender os processos da fragmentação *per se* (independente da perda de habitat *sensu*

(FAHRIG, 2017)). Desta forma, as manchas florestais com bordas naturais (ex: capões de mata) podem ser modelos úteis para entendermos estes processos. Contudo, estas manchas florestais são pouco estudadas (COELHO et al., 2018; MATTE; MÜLLER; BECKER, 2015; RIBEIRO; SANTANA; CARVALHO, 2018), além de serem negligenciadas pelos órgãos de proteção ambiental (COELHO et al., 2017, 2018).

Os capões de mata são manchas florestais formadas naturalmente em meio a uma matriz campestre, possuindo diversos tamanhos e formatos e com transição abrupta para o campo circundante (COELHO et al., 2017; RAMBALDI; OLIVEIRA, 2003; RIBEIRO; SANTANA; CARVALHO, 2018). Montanhas tropicais de baixa elevação e montanhas tropicais sem neve (entre 1000 e 3000 altitudes) fornecem bons modelos de capões de mata, pois nessas altitudes duas fitofisionomias coexistem, os campos e as florestas (APARECIDO et al., 2018; COELHO et al., 2018; FERNANDES, 2016). No Brasil, as cadeias montanhosas da Serra da Mantiqueira e da Serra do Espinhaço em altitudes acima de 1200 m (COELHO et al., 2018; RIBEIRO; SANTANA; CARVALHO, 2018; SANTANA et al., 2021) e a região do Planalto Sul-Brasileiro (BEHLING et al., 2009; MATTE; MÜLLER; BECKER, 2015) apresentam vários desses sistemas. Uma característica dessas áreas são as baixas temperaturas durante o ano e a alta umidade relativa do ar, principalmente devido ao aumento da intensidade do nevoeiro (APARECIDO et al., 2018; RIBEIRO; SANTANA; CARVALHO, 2018).

Em grandes escalas de tempo, vários fatores regulam a estabilização dos capões. As relações edáficas são um dos principais fatores nesta estabilização. Os campos estão inseridos preponderantemente em locais de solo raso e pobre em nutrientes (BENITES et al., 2003, 2007; CAMPOS et al., 2018), o que limita a expansão dos capões, pois os mesmos só conseguem se estabelecer em locais de solo mais profundo, que tenha disponibilidade hídrica e que ocorra acúmulo de nutrientes (COELHO, 2014; COELHO et al., 2017).

Além do solo, mudanças climáticas que ocorreram no passado podem ter contribuído para o isolamento dos capões, principalmente para as manchas florestais do sul do Brasil (RAMBALDI; OLIVEIRA, 2003). Com períodos de aquecimento e resfriamento do planeta os capões teriam acompanhado esses eventos com retração e expansão da floresta sobre o campo, assumindo as condições atuais (BEHLING, 1995). Outro fator regulador são os eventos de incêndios. O fogo é um fator frequente nas vegetações campestres (HOFFMANN et al., 2012b), com isso, por muitas vezes as bordas são atingidas e assim retardam a expansão das manchas florestais (COELHO et al., 2018; SILVA et al., 2019b). Porém, a intensidade e ocorrência de fogo nestas áreas tem se tornado cada vez mais frequente, com isso, os eventos de incêndios

são atualmente considerados uma das principais ameaças para conservação dos capões. O aumento da intensidade do fogo pode eventualmente levar à extinção ou redução drástica dos capões, dando espaço a manchas cada vez menores e compostas predominantemente por espécies oportunistas (COELHO, 2014; COELHO et al., 2018).

2.4. O fogo na transição campo-floresta (ambientes ecotonais)

Os ecótonos são áreas de transição entre duas ou mais comunidades, ou ainda uma zona de tensão entre duas formações vegetacionais que pode ter uma extensão linear considerável (YARROW; MARÍN, 2007). Estas zonas de transição podem ser encontrados em diferentes escalas, desde grandes ecótonos ambientais até ecótonos regionais e locais, impulsionados por fatores ambientais e bióticos (DANTAS et al., 2016; KARK; VAN RENSBURG, 2006; REHM; FEELEY, 2015). De fato, na escala regional e, em menor grau, na escala local, os fatores bióticos locais, como as interações de espécies, podem se sobrepor a fatores ambientais maiores, determinando o alcance e a distribuição das transições de vegetação (MYSTER, 2012; OLIVERAS; MALHI, 2016).

O fogo, em muitos casos, pode ser considerado determinante em áreas ecotonais, principalmente na transição de domínios savânicos para domínios florestais (MYSTER, 2012; OLIVERAS; MALHI, 2016). Nesta zona transicional existe um equilíbrio dinâmico entre o avanço da floresta e seu recuo em resposta à várias perturbações (REHM; FEELEY, 2015; ROSSATTO; HOFFMANN; FRANCO, 2009). Contudo, dependendo da frequência e intensidade dos incêndios nestas regiões, o fogo pode se tornar o principal fator regulador desta dinâmica vegetacional, gerando zonas ambientalmente adequadas que somente espécies adaptadas poderiam ocupar (HOFFMANN et al., 2012a; HOFFMANN; ORTHEN; NASCIMENTO, 2003; MÜLLER et al., 2007).

O fogo é um forte filtro ambiental promovendo uma composição, estrutura e dinâmica ecológica da vegetação específica e determinada pelo fogo (VELDMAN et al., 2015). Na ausência de fogo, a vegetação dependente do fogo sofre mudanças na composição, estrutura e dinâmica das espécies (BOND; WOODWARD; MIDGLEY, 2005; DANTAS et al., 2016). Nessa nova condição de supressão de incêndios, espécies sensíveis ao fogo se sobrepõem competitivamente às demais devido às suas vantagens fisiológicas (por exemplo, maiores taxas de crescimento), alterando o balanço entre os grupos ecológicos de espécies, a estrutura do

dossel e eliminando o componente herbáceo-arbustivo (principal combustível para ocorrência de incêndios e intensificação) (BOWMAN et al., 2009; VELDMAN et al., 2015).

Um exemplo de como o fogo funciona como filtro ambiental pode ser visto na transição entre florestas e áreas campestres adjacentes (COELHO et al., 2018). A borda (área ecotonal) de muitas destas florestas é dominada por espécies demandantes de luz e de crescimento rápido (BRAGION et al., 2018), no entanto, na ausência de incêndios florestais por longos períodos pode dar espaço para as espécies do interior da floresta ocuparem estas áreas (HOFFMANN et al., 2012b). Porém, com a volta do evento fogo espécies oportunistas e de rápido crescimento voltam ao sistema novamente (COELHO et al., 2018). Esta flutuação entre espécies nos mostra como áreas ecotonais são dinâmicas e como o evento fogo é determinante na expansão ou retração das formações savânicas e florestais. Porém, vale destacar que o fogo não é um agente determinante para formação dos campos, na verdade ele é um agente modelador destas formações (HOFFMANN et al., 2012a, 2012b; HOFFMANN; ORTHEN; NASCIMENTO, 2003).

Um paradigma ecológico emergente é que a zona de transição entre a floresta tropical e as savanas, sob as mesmas condições ambientais, podem ser considerados estados estáveis alternativos (DANTAS et al., 2016; OLIVERAS; MALHI, 2016). Existe um consenso crescente de que as savanas podem ser auto estabilizáveis por meio de um mecanismo de retroalimentação positiva entre fogo e baixa cobertura de árvores. Além disso, as copas fechadas das florestas podem impedir que o fogo ocorra, superando a vegetação herbácea inflamável e criando um microclima úmido (HOFFMANN et al., 2012b). Assim, sob determinadas condições climáticas, tanto a floresta quanto a savana podem estar presentes (OLIVERAS; MALHI, 2016).

2.5. A relação borda-interior em manchas florestais e o efeito de borda

Mesmo em pequenas escalas, como a relação borda-interior das florestas, a distribuição espacial das espécies está relacionada às condições edáficas e as variações ambientais de cada habitat (BOTREL et al., 2002; COELHO et al., 2016; WEKESA et al., 2018). Muitos trabalhos têm mostrado que quanto mais próximo da borda, as manchas florestais apresentam maior incidência luminosa, com consequente aumento da temperatura tanto do ar quanto do solo, maior exposição aos ventos, maior déficit hídrico, aumento da herbivoria e maior vulnerabilidade a ações antrópicas (HARPER et al., 2005; MAGNAGO et al., 2015; MURCIA,

1995; VAN DEN BERG; SANTOS, 2003). Estas diferenças ambientais no gradiente florestal são chamadas de efeito de borda (MAGURA; LÖVEI; TÓTHMÉRÉSZ, 2017; MURCIA, 1995; RIES et al., 2004).

Contudo, diferentes ecossistemas respondem de forma distinta aos efeitos provocados pela borda (HARPER et al., 2005; RIES et al., 2004; RIES; SISK, 2010). Os principais fatores que modulam a intensidade do efeito de borda são: a idade, origem, histórico de uso, fisionomia, orientação e tipo de matriz circundante (MURCIA, 1995; RIES et al., 2004). Dentre estes fatores, merecem destaque a idade e a origem da borda. A origem pode ser um importante direcionador do efeito de borda porque bordas criadas a partir de forças não mais operantes e mantidas por processos naturais são habitats mais antigos em comparação àquelas criadas e mantidas por atividades antropogênicas (MAGURA; LÖVEI; TÓTHMÉRÉSZ, 2017; STRAYER et al., 2003). Neste sentido, as bordas naturais tendem a apresentar uma vegetação mais densa, reduzindo a profundidade de penetração da luz solar, conseqüentemente reduzindo a distância dos efeitos de borda (COELHO et al., 2016; MAGURA; LÖVEI; TÓTHMÉRÉSZ, 2017).

Além das variações ambientais, o tamanho e a forma das manchas florestais também são métricas importantes para descrever os padrões ecológicos de comunidades de plantas (ARELLANO-RIVAS; DE-NOVA; MUNGUÍA-ROSAS, 2018; MENDES; RIBEIRO; GALETTI, 2016), a conformação das manchas pode influenciar a quantidade de borda e, assim, aumentar ou diminuir o efeito de borda (HARPER et al., 2005; MURCIA, 1995). Com a diminuição no tamanho da mancha florestal, a pressão externa na área central aumenta e o efeito de borda é intensificado (FERRANTE et al., 2017; LAURANCE; CURRAN, 2008; MAGNAGO et al., 2015). Já a forma está relacionada com a circularidade do fragmento, manchas com formas irregulares têm maior razão perímetro-área e maior área relativamente afetada (ARELLANO-RIVAS; DE-NOVA; MUNGUÍA-ROSAS, 2018). Com isso, manchas florestais muito pequenas ou muito irregulares são totalmente afetadas pelo efeito de borda, nestas condições pode ocorrer diminuição na riqueza de espécies e aumento na proporção de espécies generalistas, além de alteração na estrutura da vegetação em toda floresta (LAURANCE; CURRAN, 2008; MUNGUÍA-ROSAS; MONTIEL, 2014; MURCIA, 1995).

Segundo Harper et al. (2005), dependendo da mancha florestal, a distância do efeito de borda pode variar de dez a mais de cem metros. Já Murcia (1995) comenta que, no geral, as diferenças entre borda e interior tendem a desaparecer nos primeiros 50 metros do fragmento florestal. Tais dados são para fragmentos com bordas de origem antropogênica, onde na maior

parte das vezes são formadas de forma abrupta, além de serem expostas constantemente a impactos diretos (corte seletivo, pastagem) e indiretos (dissipação de pesticidas) (MAGURA; LÖVEI; TÓTHMÉRÉSZ, 2017). Contudo, a magnitude do efeito de borda em manchas florestais com bordas naturais é pouco conhecida. Desta forma, um esforço para entender os processos que governam as diferenças entre borda e interior nestas áreas torna-se necessário.

As diferenças bióticas e abióticas no gradiente florestal podem desencadear reflexos diretos no desenvolvimento das plantas, provocando alterações na estrutura e diversidade (taxonômica e funcional) da comunidade (BRAGION et al., 2018; COELHO et al., 2016; SAMPAIO; SCARIOT, 2011; SILVA et al., 2019a; WEKESA et al., 2019). As variações atuam como filtros ambientais e habitats próximos, mas com características distintas, podem apresentar diferentes arranjos de espécies (ERDŐS et al., 2019; OOSTERHOORN; KAPPELLE, 2000; VAN DEN BERG; OLIVEIRA-FILHO, 1999). O habitat de borda, por exemplo, recebe mais luz, pois além de ter um dossel mais baixo, há penetração de luz lateral através da paisagem aberta circundante, com isso, espécies demandantes de luz tendem a ocupar estes habitats. Em contrapartida, a menor disponibilidade de luz no interior florestal aumenta a abundância de espécies tolerantes à sombra (BRAGION et al., 2018; VAN DEN BERG; SANTOS, 2003). Além destas diferenças, as variações entre os habitats também podem alterar a dinâmica da comunidade. As bordas possuem maior estresse climático e estão mais sujeitas a eventos de incêndios, com isso, apresentam maior mortalidade de espécies e conseqüentemente menor acúmulo de biomassa em relação ao interior florestal (D'ANGELO et al., 2004; HARPER et al., 2005; SILVA et al., 2019b).

2.6. Traços e diversidade funcional

Sob influência de diferentes condições ambientais, as espécies apresentam várias mudanças de ordem morfológicas, anatômicas, fisiológicas e reprodutivas (CASENAVE; PELOTTO; PROTOMASTRO, 1995; VALLADARES; GIANOLI; GÓMEZ, 2007). A borda e o interior das florestas são considerados habitats tipicamente contrastantes devido aos fatores ambientais a que estão condicionados (BRAGION et al., 2018; KOLODZIEJEK, 2014). Desta forma, tornam-se relevantes modelos de estudo para entender as mudanças das espécies em resposta ao meio (DA COSTA et al., 2020; SILVA et al., 2019a). Habitats de borda, por exemplo, estão mais sujeitos a pressões das áreas abertas adjacentes (D'ANGELO et al., 2004; GUIMARÃES et al., 2008; SILVA et al., 2019b). Com isso, apresentam espécies com

características de rápida aquisição de recursos (aquisitivas) e, portanto, de crescimento rápido (BRAGION et al., 2018; WEEMSTRA et al., 2016; WRIGHT et al., 2004, 2010). Em contrapartida, o interior florestal, além de apresentar maior estabilidade climática, possui menor incidência de luz (D'ANGELO et al., 2004; MAGNAGO et al., 2015), favorecendo organismos com estratégias conservativas, como baixas taxas de fotossíntese e respiração, crescimento lento, mas elevada eficiência no uso de recursos, e, conseqüentemente, com maior sobrevivência dos indivíduos (WEEMSTRA et al., 2016; WRIGHT et al., 2010). Porém, este padrão esperado pode ser alterado em decorrência dos fortes filtros ambientais (ASEFA et al., 2017; WRIGHT et al., 2010).

As diferenças estruturais a nível individual entre as espécies podem ser mensuradas através dos traços funcionais (CORNELISSEN et al., 2003; VIOLLE et al., 2007). De forma geral, os traços funcionais ou atributos funcionais podem ser definidos como características com influência potencialmente significativa no estabelecimento ou sobrevivência de um organismo em seu ambiente natural (VIOLLE et al., 2007). Os traços funcionais podem ser entendidos também como indicadores/ provedores dos serviços ecossistêmicos, com isso, uma maior amplitude de traços funcionais em uma comunidade indicará mais serviços prestados (CARLUCCI et al., 2020; DÍAZ et al., 2007, 2013).

Os traços podem ser medidas categóricas, quando pertencem a uma classe (dispersão zoocórica ou anemocórica; plantas pioneiras ou não pioneiras) ou medidas contínuas, quando infinitos valores são possíveis (área foliar, espessura da folha, projeção da copa, altura, densidade da madeira, etc) (PÉREZ-HARGUINDEGUY et al., 2013). Assim sendo, torna-se possível agrupar as espécies de acordo com as características morfofisiológicas que elas apresentam, uma vez que a similaridade funcional pode corresponder a uma resposta comum à ação dos filtros ambientais (CORNELISSEN et al., 2003; GRIME, 2006). Vale ressaltar que não existe um traço funcional mais importante a ser incorporado em um estudo. Porém, deve-se tomar cuidado no uso de alguns, pois o traço precisa ser realmente funcional, ou seja, ter demonstrável efeito sobre os processos ecossistêmicos e precisa relacionar-se com o que pretende investigar (MLAMBO, 2014; ROSADO et al., 2004; VIOLLE et al., 2007).

Uma forma de medir a variação de traços funcionais de uma comunidade é através da diversidade funcional (CIANCIARUSO; SILVA; BATALHA, 2009; LAURETO; CIANCIARUSO; SAMIA, 2015; TILMAN, 2001). A diversidade funcional mede as diferenças entre os organismos através de características que influenciam o funcionamento do ecossistema (TILMAN, 2001). Desta forma, uma comunidade terá maior diversidade funcional quando uma

amplitude maior de dimensões dos recursos são exploradas pelos organismos, em outras palavras, há uma maior diversidade de nichos ecológicos. Ou ainda, assumindo que os organismos podem ser categorizados como pertencentes a grupos que diferem em traços relevantes para o funcionamento do ecossistema, uma maior diversidade de grupos funcionais deve correlacionar-se com maior diversidade funcional (PETCHEY; GASTON, 2002, 2006; TILMAN, 2001).

Além disso, a diversidade funcional pode ser uma importante ferramenta para tentar entender os processos ecológicos que determinam o funcionamento das comunidades (CIANCIARUSO; SILVA; BATALHA, 2009; MOUCHET et al., 2010). Pois a forma como os organismos utilizam os recursos reflete na diversidade funcional, desta forma, é possível testar se os filtros ambientais ou a competição, por exemplo, são processos importantes na organização da comunidade (GÖTZENBERGER et al., 2012; MOUCHET et al., 2010). Ou seja, uma comunidade com fortes filtros ambientais, em que poucos organismos conseguem se manter, terá uma pequena variação nos traços funcionais e conseqüentemente menor diversidade funcional. Em contrapartida, uma comunidade com maior diversidade funcional indica maior variação nos traços funcionais, possivelmente resultante da competição ao longo do tempo reduzindo a sobreposição de nichos e aumentando a especialização dos organismos em determinados recursos (CIANCIARUSO; SILVA; BATALHA, 2009).

Assim como outras medidas de diversidade (taxonômica, filogenética), existem inúmeros índices para calcular a diversidade funcional (LALIBERTE; LEGENDRE, 2010; MASON et al., 2005; MOUCHET et al., 2010). A escolha do melhor índice está relacionada a quantidade de traços utilizados, se são qualitativos ou quantitativos, a riqueza de espécies e a distribuição das abundâncias das espécies na comunidade (CALAÇA; GRELE, 2016). Portanto, os questionamentos a serem respondidos no trabalho devem levar em consideração todos estes pontos.

2.7. Variação intraespecífica de traços funcionais

A necessidade de entender como as características das espécies influenciam os processos ecossistêmicos fez com que a ecologia funcional ganhasse papel de destaque nos estudos ecológicos das últimas décadas (CALAÇA; GRELE, 2016; SIEFERT et al., 2015). Medir os traços funcionais e avaliar sua variação dentro e entre comunidades proporcionou um novo caminho para investigar os padrões de estruturação de comunidades ecológicas (KRAFT

et al., 2015; SIEFERT et al., 2015). Inclusive vários bancos de dados com traços funcionais de espécies vegetais foram criados para colaborar com os trabalhos (CHAVE et al., 2009; FRASER, 2020). Nestes casos, é assumido a priori que a variação nos traços funcionais dos indivíduos da mesma espécie de diferentes habitats é irrelevante para diversidade funcional (CIANCIARUSO et al., 2009).

Contudo, alguns estudos tem mostrado que indivíduos da mesma espécie, mesmo em pequenas escalas, são capazes de alterar caracteres fenotípicos ao longo de gradientes ambientais em decorrência da interação com o ambiente (BORGES et al., 2018; SILVA et al., 2019a; VERGARA-GÓMEZ; WILLIAMS-LINERA; CASANOVES, 2019). Além disso, é indicado que a variabilidade intraespecífica exerce papel importante no funcionamento das comunidades (ALBERT et al., 2010). A variação intraespecífica é resultado da variação genética e da plasticidade fenotípica (ASPINWALL et al., 2015; BENOMAR et al., 2016; PRITZKOW et al., 2019). Entende-se por plasticidade fenotípica a capacidade de um genótipo expressar diferentes fenótipos (BRADSHAW, 2006; VALLADARES et al., 2014; VALLADARES; GIANOLI; GÓMEZ, 2007). A variação nos traços funcionais permite as espécies ampliarem a extensão do nicho, refletindo diretamente na captura de recursos e sobrevivência, representando uma importante adaptação das plantas (ALBERT et al., 2010; BRADSHAW, 2006; CIANCIARUSO; SILVA; BATALHA, 2009). As espécies que possuem maior potencial de variação em nível de indivíduo possuem maior capacidade adaptativa a ambientes instáveis e heterogêneos (FRÉJAVILLE et al., 2019; PÉREZ-RAMOS et al., 2019).

Em alguns casos, os traços funcionais de indivíduos da mesma espécie podem diferir tanto quanto entre espécies distintas (ALBERT et al., 2012; UMAÑA; SWENSON, 2019). Neste sentido, em uma meta-análise global para verificar a extensão relativa da variação intraespecífica dentro e entre comunidades de plantas verificou-se variações de 25% dentro das comunidades e 32% entre comunidades em média. As maiores variações foram verificadas nos traços funcionais que utilizam características inteiras das plantas, como por exemplo, altura máxima, em comparação aqueles ao nível de órgão (variação foliar) (SIEFERT et al., 2015).

A importância da variação intraespecífica para o funcionamento das comunidades é indiscutível, porém, nenhum dos métodos para estimar a diversidade funcional fornece uma forma clara para incorporar este nível de variação (ALBERT et al., 2012; PETCHEY; GASTON, 2006). A maioria destes métodos, principalmente os de múltiplos traços, usam os valores médios das características das espécies (UMAÑA; SWENSON, 2019). Nesse sentido, ao negligenciar a variação intraespecífica ou utilizar valores médios nos índices de diversidade

funcional pode-se estar gerando interpretações equivocadas, afetando negativamente as inferências sobre o funcionamento das comunidades (CIANCIARUSO et al., 2009; SIEFERT et al., 2015).

3. CONSIDERAÇÕES FINAIS

No presente estudo foi possível verificar que a borda e o interior de manchas de florestas naturais (capões de mata) são habitats altamente contrastantes em termos de estrutura, variáveis edáficas e diversidade funcional. Neste sentido, as manchas naturais tornam importante modelo para entendimento sobre o efeito de borda, principalmente quando se trata da fragmentação *per se* (independente da perda de habitat). Além disso, foi demonstrado que o tamanho e forma das manchas são fatores que devem ser levados em consideração nestes estudos, pois são importantes direcionadores de mudanças na comunidade arbórea.

As diferenças encontradas são reflexos das condições ambientais que cada habitat está sujeito. Desta forma, as bordas por estarem em contato direto com o ambiente externo tornam-se um habitat com fortes filtros ambientais e conseqüentemente mais seletiva em termos de arranjo de traços funcionais. Esta peculiaridade justifica o padrão encontrado nas métricas funcionais, ou seja, menor diversidade funcional e indivíduos com traços funcionais que amenizam o estresse causado pela borda, como redução da área foliar específica (AFE) e aumento da densidade da madeira. Porém, estas diferenças só ficaram evidentes quando levado em consideração a variação intraespecífica dos traços funcionais entre os habitats. Com isso, é importante ressaltar que negligenciar essa variação nos estudos de diversidade funcional, especialmente aqueles que incorporam variáveis quantitativas, pode resultar em interpretações errôneas sobre os padrões ecológicos.

Vários estudos ainda são necessários para melhor compreender os principais padrões e processos que governam os capões de mata com bordas naturais, principalmente em ambientes montanhosos devido a peculiaridade destas áreas e a escassez de trabalhos. Neste sentido, trabalhos que buscam entender o comportamento dos capões em diferentes condições ambientais de clima e solo, somado ao acompanhamento da dinâmica florestal para tentar compreender se são áreas que estão expandindo, retraindo ou estáveis no espaço ganham importância. Além disso, traçar um paralelo entre as principais abordagens filogenéticas e funcionais para compreensão dos processos ecológicos que regulam estas comunidades. Ressalto aqui novamente a importância da junção de esforços para realização de estudos com

os capões de mata, pois são regiões singulares, com uma riqueza de espécies pouco compreendida e ainda servem de modelo para aplicação de vários conceitos ecológicos. Porém, são áreas negligenciadas pelos órgãos públicos e que se encontram ameaçadas por diferentes fatores, sejam políticos (enfraquecimento da legislação e dos órgãos vigentes de proteção ambiental) ou ecológicos.

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SEGUNDA PARTE – ARTIGOS

ARTIGO 1

Edge effects in forest patches surrounded by native grassland are also dependent on patch size and shape

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Edge effects in forest patches surrounded by native grassland are also dependent on patch size and shape

Abstract

Our knowledge of biodiversity responses to fragmentation comes from human-driven fragmentation processes. However, evaluating forest patches with natural edge can produce useful models to understand how the micro-environmental gradient between forest edge and interior shapes the plant communities, regardless habitat loss. Here, we tested how forest edges and interiors differ in soil characteristics, communities' structure and diversity metrics, and the extent to which these differences are related to forest size and shape of patches. We present data of ten tropical montane cloud forest patches surrounded by native non-forest vegetation (highland grasslands) of southeast Brazil. In each forest, we established five plots right on the edge and five randomly distributed over the forest interior. Our dataset covers a total of 5495 trees, and the main findings showed that patches with natural edges are also influenced by the edge effect, affecting the structure, species composition and soil variables. We found that with the increase in distance from the forest edge, the soils became more acid, with greater accumulation of organic matter, phosphorus, silt and sand, in contrast, the content of total exchangeable bases and clay decreased. When accounting for the effect of patch size and shape in the relationships between forest habitat and the structural community metrics, tree density and upper 95-percentile stem diameter tended to be higher in larger patches. In contrast, aboveground biomass and median stem diameter were positively related to patch shape in forest interiors. In addition, species composition showed marked differences between habitats, but rarefied species richness and Fisher's diversity index were higher, in the interior, only in large patches. These results indicate that besides differences between forest habitats, with increasing patch size and circularity, the differences become more pronounced. We would like to highlight

that in conservation and management decisions, peculiarities of each habitat must be taken into account, with techniques that assess the surrounding matrix (man-made or natural) and that consider the edge and the interior as distinct habitats.

Keywords: edge-interior transition; natural edge; sharp ecotone, soil variables

1. Introduction

Forest fragmentation is generally thought of as a factor of habitat degradation and a primary driver of biodiversity loss worldwide (Haddad et al., 2015). Studies of forest fragmentation are mainly based on comparisons between continuous and fragmented landscapes or among forest fragments of different sizes. In this sense, our understanding of the fragmentation effects on biodiversity is highly linked to habitat loss (Fahrig, 2017). In addition to habitat loss, forest fragmentation changes the environmental conditions, community structure, and composition close to the edge of the patches, which have been termed ‘edge effects’ (Murcia, 1995; Pardini et al., 2017). To understand the fragmentation process per se (i.e., regardless of habitat loss, Fahrig, 2003) we must evaluate how the ecological and ecosystem processes differ between the forest edge and interior (Laurance, 2002; Wang et al., 2020). However, our knowledge of biodiversity responses to fragmentation comes from human-driven fragmentation processes (da Silva et al., 2019; Fahrig, 2017). Evaluating forest patches with natural edges can produce useful models to understand how the micro-environmental gradient between forest edge and interior shapes the plant communities despite habitat loss (da Silva et al., 2019). Here, we evaluate the extent to which the classical human-driven edge effects also hold for forest patches with natural edges.

From the forest interior towards the edge, independently if the forest patch is natural or man-made, species are exposed to a gradient in microclimatic conditions, such as increased light availability, temperature variation, wind exposure, atmospheric water stress, and vulnerability to fire events (Erdős et al., 2018; Harper et al., 2005; Magnago et al., 2015; van den Berg and Santos, 2003). These shifts in microclimatic conditions directly affect the establishment and development of plants, and hence, nearby habitats (edge and interior) within a forest patch can be markedly different in terms of structure, diversity, and anatomical and functional metrics (Coelho et al., 2016; da Costa et al., 2020; Erdős et al., 2019; Wekesa et al., 2019). At the edge, tree density is usually high but composed by small-statured trees (i.e., low stem diameter and height), which reduces aboveground biomass stocks (Silva et al., 2019). Due to the high light availability, the edge community is dominated by light-demanding species with high growth and low survival rates (Bragion et al., 2018; Magnago et al., 2015). In contrast, the shaded-humid condition in the forest interior favors the dominance of long-lived and shade-tolerant species (Bragion et al., 2018), that grow slowly but can reach taller heights and larger stem diameters, and hence, increase canopy height and aboveground stand biomass (Silva et al., 2019).

The magnitude and distance of the edge effects in forest patches can vary from ten to more than one hundred meters inside forests, according to the local conditions such as the age of the edge (Harper et al., 2005; Ries et al., 2004), regional climate (Meeussen et al., 2020), vegetation type (Murcia, 1995), fragment size and shape (Galanes and Thomlinson, 2009; Laurance and Curran, 2008), and land use of surrounding matrix (Melito et al., 2018; Moura et al., 2012). For instance, older edges tend to have denser vegetation, which reduces the light incidence and, consequently, the distance reached by the edge effects (Harper et al., 2005; Ries et al., 2004). Differences in the environmental filters between the forest edge and interior are also related to the shape and size of forest patches, influencing the relative amount of edge and

core areas within a forest patch (Arellano-Rivas et al., 2018; Melito et al., 2018). With increasing patch size, external pressure in the forest interior decreases and the edge effect is reduced (Laurance and Curran, 2008; Magnago et al., 2015). The shape is related to the circularity of the forest patch, in which patches with more irregular shapes have a higher perimeter-area ratio and then, have relatively more area affected by the edge effect than more circular patches (Arellano-Rivas et al., 2018).

However, most studies are on man-made forest edges (Harper et al., 2005; Magnago et al., 2015; Wekesa et al., 2019), and the extent to which forest patches surrounded by natural matrix are exposed to edge effects is still unclear. These natural forest patches have old edges with sharp transitions to open physiognomies (Coelho et al., 2016, 2018b; Ribeiro et al., 2018). Natural edge is common in seasonal savannas and grasslands (Coelho et al., 2016; Hoffmann et al., 2009), but also appears in tropical mountains (altitude ranging from 1000 to 3000 m) where forest and grassland occur together under low human-impact condition (Aparecido et al., 2018; Coelho et al., 2018b; Fernandes, 2016). In tropical montane forests, the low temperatures over the year and the high relative humidity, due to the constant presence of fog (Aparecido et al., 2018), can reduce the differences in the environmental filters between the forest edge and interior.

Edaphic characteristics are also important factors conditioning the structure and limits of forest patches with the surrounding open natural vegetation (Coelho et al., 2018b; van den Berg and Santos, 2003). When these forest patches are inserted in a grassland matrix (Coelho et al., 2018b; Erdős et al., 2019) with shallow and nutrient-poor soils, they are frequently restricted to the valleys with deeper soils and higher water and nutrient availability (Coelho et al., 2018a; Ribeiro et al., 2018) (Fig. 1). In addition to edaphic variables, fire is a modulator of these systems, regulating the expansion and retraction of patches over the surrounding open vegetation (Coelho et al., 2018b; Silva et al., 2019).

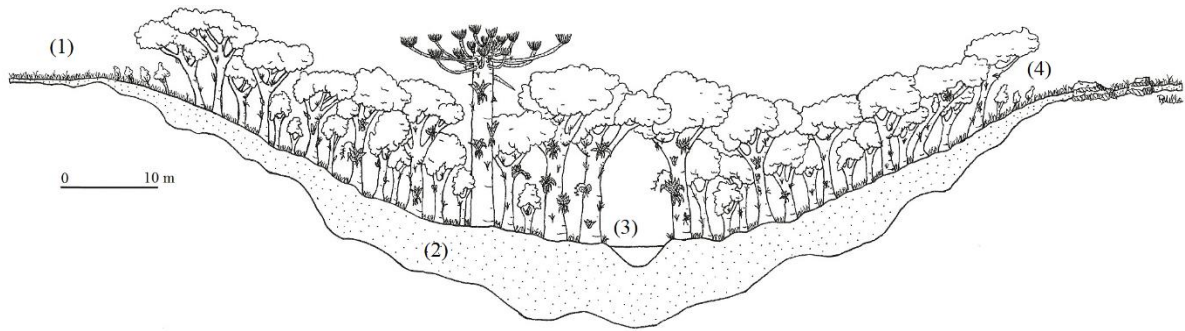


Figure 1: Vegetation profile of tropical montane cloud forest patch surrounded by native grasslands. (1) highland grasslands; (2) soil depth; (3) watercourse or spring; (4) sharp transition (edge) between forest and native grassland.

In this study, we evaluated how forest edges and interiors differ in community structure and diversity and the extent to which these differences are related to forest size and shape and soil characteristics. We present data of ten tropical montane forest patches with natural edge with grasslands, and address the following hypotheses: (i) Considering that forest interiors are situated in the lower sections of valleys, they are supposed to be the recipient of any particles transported from the forest edges (upside of valleys), and therefore, agreeing with other studies (Rodrigues et al., 2007; Silva et al., 2019; Terra et al., 2018), we expected the interiors to have higher levels of clay, soil nutrients and organic matter (OM). We also expected, as a result of a higher concentration of aluminum and organic matter, lower pH in forest interiors compared to the forest edge. (ii) If the edge effects work in tropical natural forest patches in the same way as in anthropogenic forest fragments, we expected the forest edge to have higher tree density composed of small-statured trees, lower aboveground biomass, and lower species richness/diversity. In addition, we expected higher dissimilarity in species composition between the habitats (edge vs. interior) within the same forest patch than among the same habitat in different forest patches; (iii) Differences between the forest edge and interior will be greater in larger patches with more circular shapes because they have low edge-to-interior ratios.

2. Material and methods

2.1. Study areas

We carried out this study in the Serra do Papagaio State Park (PESP), a protected area located in the Serra da Mantiqueira, Southeastern Brazil (22°7'34"S, 44°44'54"W) (Fig. 2a). The park covers an area of 22,917 hectares and has been described as one of the best-preserved remnants of the Brazilian Atlantic Forest. The Atlantic Forest is a global biodiversity hotspot for conservation priorities (Myers et al., 2000) due to its high species endemism and actual degradation (less than 15% of the original cover remaining (SOS Mata Atlântica, 2019)). The PESP harbors a variety of plant physiognomies, from open grasslands with few shrubs and trees to dense cloud forests and alluvial subtropical forests with the marked presence of the species *Araucaria angustifolia* (Bertol.) Kuntze (Ribeiro et al., 2018; Santana et al., 2020). The studied forest patches are classified as Tropical Montane Cloud Forest (TMCF) (sensu Fahey et al., 2016; Pompeu et al., 2018) and are surrounded by native non-forest vegetation (mostly highland grasslands and, to a lesser extent, wetlands). Highland grasslands in the PESP occur in lithosols (shallow soils consisting of imperfectly weathered rock fragments), characterized by low organic matter levels. In contrast, TMCF occurs in cambisols and histosols, that have at least an incipient subsurface soil formation and high accumulation of organic matter and moisture in the upper soil layers (IUSS Working Group WRB, 2015; Ribeiro et al., 2018). The forest edges with grasslands are very sharp, and the grasslands close to the edge are often dominated by the shrubs *Baccharis platypoda* DC and *Croton alchorneicarpus* Croizat (Fig. 2 b and c).

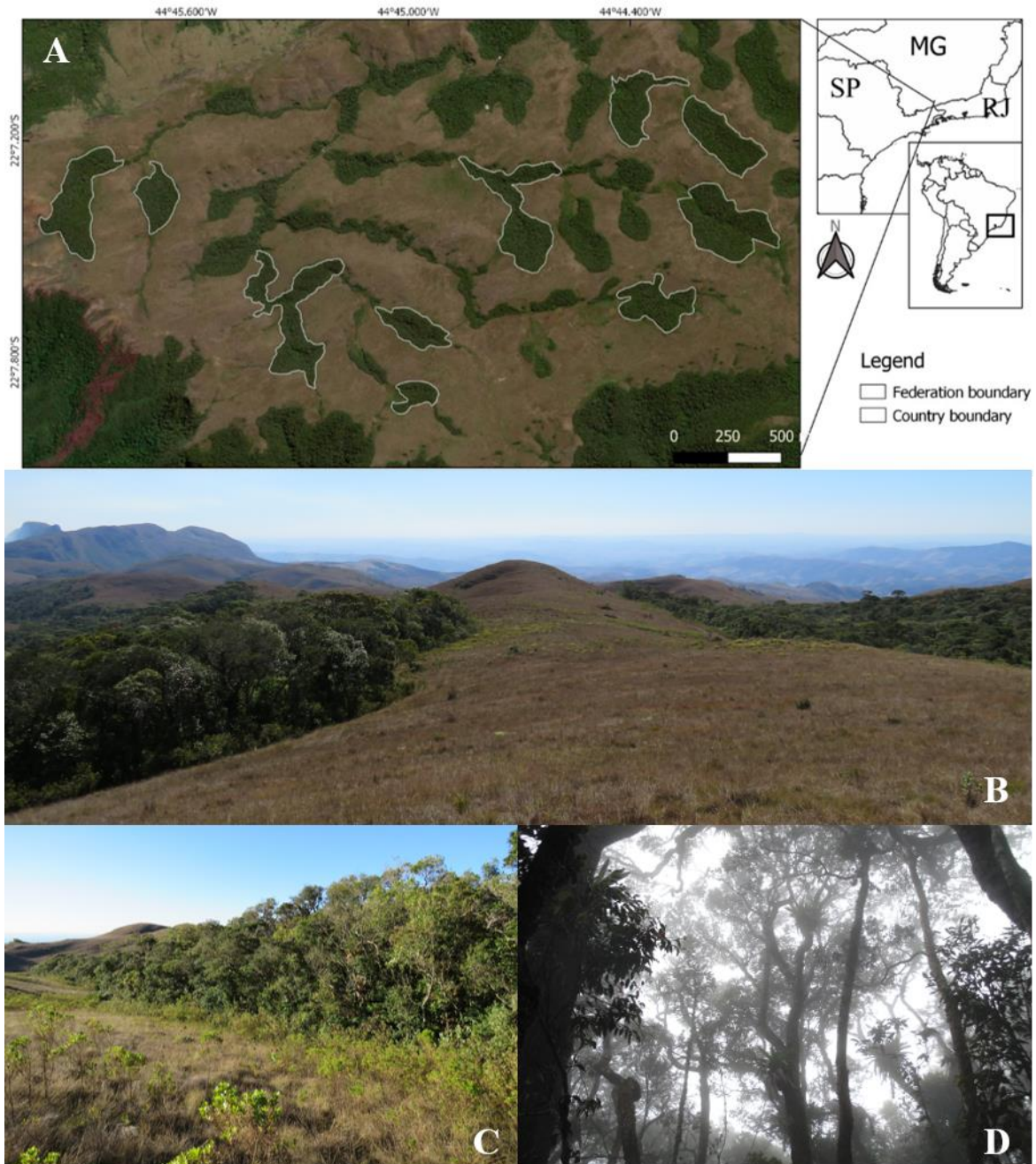


Figure 2: **A** – Location of the study area with delimitation of the 10 patches of tropical montane cloud forest, sampled in white. MG (Minas Gerais), SP (São Paulo) and RJ (Rio de Janeiro) are states of Brazil. **B** – **D**: Tropical montane cloud forest patches surrounded by highland grasslands of Serra do Papagaio State Park. **B** and **C**: – external views of the patches and the abrupt transition from the natural grassland to the forest. **D**: Forest interior, showing canopies immersed in fog.

The altitude of the studied forest patches was between 1800 and 2000 m. The region experiences a subtropical highland climate (Cwb type according to the Köppen climate classification), with rainy summers and cold and dry winters. We obtained climatic data from the WorldClim rasters dataset, with a 1 km² resolution (Hijmans et al., 2005), available at <https://www.worldclim.org/>. The mean annual precipitation is 2060 mm, of which 80% is concentrated between October and March, but there is no fully dry month. In the driest months, the precipitation is around 30 and 90 mm. As the mist formation is constant over the year, some additional precipitation can result from the condensation of water droplets on the surface of plants, in a process called horizontal rain (Bruijnzeel et al., 2010, 2011). The mean annual temperature is 13.8° C. The minimum temperatures in the winter are usually between 0° C and 10° C, with occasional frosts. The summer is mild, with temperature, in the hottest days, usually lower than 30° C.

2.2. Vegetation and soil sampling

The TMCF patches were mapped using satellite images and information gathered on fieldwork. We randomly selected 10 forest patches ranging from 2 to 11 ha (Figure 2a) (Appendix A). In each forest, we established 10 permanent sample plots (20 m × 10 m), with five allocated right on the forest edge (longer side parallel to the limit between the forest and the grassland), and five randomly distributed over the forest interior (ranging from 20 m to 117 m from the limit with grassland, depending on the forest size). Data from interior plots were obtained from Ribeiro et al. (2018). Our dataset covers a 2 ha sampling effort (1 ha for each forest habitat) and a total of 5495 trees, belonging to 107 species, 54 genera and 34 families (Appendix B).

We sampled all trees in the plots with a diameter at breast height (DBH, measured at 1.3 m above the ground) \geq 5cm. Trees were tagged, had DBH measured, height estimated, and

identified to species level, whenever possible. We carried out the botanical identification using specialized literature, consulting with specialists, and comparing the material with the collection of the Leopoldo Krieger herbarium (CESJ) from the Federal University of Juiz de Fora (UFJF), following the proposal of the Angiosperm Phylogeny Group IV (2016) and the Pteridophyte Phylogeny Group (PPG, 2016, for tree fern species). The synonymy of the species was checked in the Brazilian Flora Species List 2020 (BFG, 2018).

To evaluate soil chemical and physical attributes, we collected soil samples from 0 to 20 cm of depth at five fixed locations distributed in each plot (at plot vertices and in the center). We mixed and homogenized the five soil samples, resulting in a single one for each plot, which we sieved with a 2-mm sieve to remove roots and stones and air-dried for 24 h. The following soil variables were obtained in the analyses: pH (distilled water solution), phosphorus and potassium content (P and K⁺ in mg dm⁻³, Mehlich I extraction method), calcium, magnesium and aluminum content (Ca²⁺, Mg²⁺, and Al³⁺, in cmol dm⁻³, extracted using a KCl 1 mol L⁻¹ solution), total exchangeable bases (TEB, the sum of base cations Ca²⁺, Mg²⁺, and K⁺), organic matter (OM in dag kg⁻¹, Walkley Black method), and sand, silt and clay content (in percentage (%), pipette method).

2.3. Forest patch size and shape

We estimated the size of each forest patch using Google Earth Pro, keeping a fixed view-point height of 2500 m. Patch shape was estimated with the circularity index (CI) (Chaturvedi, 1926 apud Oliveira et al., 2005):

$$CI = \frac{40000 * \pi * A}{P^2} ;$$

in which A represents the patch area, measured in hectare (ha), and P represents the perimeter of the polygon measured in meters (m). The index values closer to 1 represent forest patches with a shape close to a circle ($CI = 1$, perfectly circular).

2.4. Forest structure and species diversity

To describe forest structure, we evaluated six variables per plot: tree density (trees ha⁻¹), aboveground biomass (AGB, Mg ha⁻¹), median tree height (H_{med} , m), median stem diameter (DBH_{med} , cm), upper 95-percentile tree height (H_{95} , m) and upper 95-percentile stem diameter (DBH_{95} , cm). The AGB at the plot level was calculated as the sum of the AGB of all trees. For each sampled tree, we calculated the AGB using the allometric formula: $AGB = 0.0673 \times (WD \times DBH^2 \times H)^{0.976}$ (Chave et al., 2014), in which DBH is the stem diameter at breast height (cm), H is tree height (m) and WD is wood density (g cm⁻³). We obtained wood density (WD) using a segment (at least 7 cm in circumference and 10 cm in length) of at least five individuals of each species removed from a fourth-order branch. After removing its bark, we submerged the branch in water for three days. We measured the volume of the samples using an analytical balance with an accuracy of 0.001g, applying the water-displacement method (Chave, 2006; Falster and Westoby, 2005). Subsequently, we dried the branches in an oven at 70° C for 72 hours and measured their dry mass on an analytical balance. The wood density was then calculated by the ratio between the dry mass and the volume of displaced water. We recognize that the ideal is the collection of wood from the main trunk, but because of the impossibility of collecting through this method due to the study area being a protected area, we chose to collect the branches, which is also a form of collection accepted in the standardized protocol for functional traits (Pérez-Harguindeguy et al., 2013).

To describe species diversity, we evaluated rarefied species richness (Srar, from a random sampling of 29 trees, as this number was found in the plot with the lowest number of

trees) and Fisher's alpha diversity index. The Fisher's alpha index was calculated using the following equation: $S = \alpha * \ln(1 + N/\alpha)$, where S is the number of species, N is the number of individuals, and α is Fisher's alpha (Fisher et al., 1943). We used rarefied species richness (formula available at Hurlbert (1971)) instead of species richness to account for the confounding positive effect of tree density in species richness. These variables were calculated using the 'vegan' package (Oksanen et al., 2017) in the R software (R Development Core Team, 2017).

2.5. Data analysis

To evaluate the differences in soil chemical and physical contents (Clay, Silt, Sand, pH, P, K, Ca, Mg, Al, TEB, OM) between forest habitats (edge and interior), we used generalized linear mixed models (GLMMs) including forest habitat as a fixed factor and each of the soil variables as response variables as follow: $\text{Soil} = \text{Habitat} + (1 | \text{Patch})$. We included the forest patch as a random effect to account for the nestedness of the plots within each forest patch. In this case, we were able to account for the random variability across the forest patches considering our hierarchical sampling structure (each patch has an edge dataset and an interior dataset, Zuur et al., 2009). We fitted the GLMMs using the Gamma-family (non-negative continuous data) error distribution and respective links (normal-identity, log or inverse). To illustrate soil variations between forest habitats, we conducted a principal component analysis (PCA) using eleven edaphic variables (Clay, Silt, Sand, pH, P, K, Ca, Mg, Al, TEB, OM). For this, the "PCA" function of the FactoMineR package was used (Husson et al., 2020). The variables were standardized, dividing them by their standard deviations to avoid the effect of different units of measurement and, then, the ordering was performed in a correlation matrix. Moreover, to evaluate whether the variation in soil content in the interior plots was related to their distance from the forest edge, we performed GLMMs including distance to the edge as a

fixed factor, each of the soil variables as response variables, and the forest patch as a random factor.

To evaluate the differences in forest structure (AGB, H_{med} , H_{95} , DBH_{med} , and DBH_{95}) and species diversity (Srar and Fisher diversity) between forest habitats, we performed a similar GLMM approach used in soil comparisons, but this time including forest habitat in interaction with forest size and shape.

We evaluated the differences in species composition between forest habitats using the permutational multivariate analysis of variance (PERMANOVA) and the Horn index (9999 permutations). PERMANOVA is a non-parametric multivariate test used to compare groups based on a distance index, which facilitates the analysis of beta diversity (variation in species composition) across spatial or temporal scales (Anderson, 2017). To this aim, forest habitats (edge and interior) were the groups among the permutations occurs. Horn index (based on the Hill numbers) weighs each species according to its abundance but is less sensitive to dominant species than other indices (Magurran, 2004). Horn similarity index values range from 0 (non-overlapping species composition between forest habitats) to 1 (same species composition between forest habitats). We illustrated the differences in species composition between forest habitats using a non-metric multidimensional scaling (nMDS, stress values = 0.23, a low value reflecting acceptable goodness-of-fit, Clarke et al., 2014). We compared the species relative abundance in forest habitats using SIMPER (Similarity percentages, based on Horn similarity index), a dissimilarity test that determines the degree that each species contributes to the differences in assemblage species composition (Clarke et al., 2014).

Statistical analyses were performed using the R software (R Development Core Team, 2017) and the following packages: lme4 (Bates et al., 2014), lmerTest (Kuznetsova et al., 2016), multcomp (Bretz et al., 2015), and vegan (Oksanen et al., 2017).

3. Results

Soil chemical and physical attributes were significantly different between forest habitats, except for soil K^+ (Table 1). The soil in the forest edge had higher pH, Ca^{2+} , Mg^{2+} , TEB, and clay content compared with the forest interiors. By contrast, soil in the forest interior had higher P, Al^{3+} , organic matter, and silt and sand content (Table 1). Overall, the edaphic gradient between forest habitats were confirmed by the PCA (Fig. 3), which first two axes together explained 67% of the variance related to the soil variables under study (Appendix C). Considering only the interior plots, distance from the forest edge was negatively related to pH, Ca^{2+} , Mg^{2+} , TEB, and clay content, and was positively related to P, Al^{3+} , organic matter, and silt and sand content (Table 1).

Table 1: Comparison of soil physical and chemical attributes (mean values \pm standard deviation) between forest edge and interior and results of model, evaluating the effect of distance from the edge, in the soil attributes, in ten tropical montane cloud forests surrounded by native grasslands. Clay, silt and sand content (in %), pH (in H_2O), phosphorus and potassium (P and K^+ in $mg\ dm^{-3}$), calcium, magnesium and aluminum content (Ca^{2+} , Mg^{2+} and Al^{3+} , in $cmol\ dm^{-3}$), total exchangeable bases (TEB, as the sum of base cations Ca^{2+} , Mg^{2+} and K^+) and organic matter (OM in $dag\ kg^{-1}$). Abbreviation: Coef. Standardized multiple regression coefficient.

Variables	Edge	Interior	p-value	Distance of the edge	
				Coef.	p-value
Clay	29.88 ± 3.81	18.00 ± 3.56	< 0.01	-11.880	< 0.01
Silt	10.76 ± 1.48	18.88 ± 2.75	< 0.01	1.069	< 0.01
Sand	59.36 ± 4.52	63.16 ± 4.52	< 0.01	3.800	< 0.01
pH	4.33 ± 0.19	3.92 ± 0.25	< 0.01	-0.007	< 0.01
P	5.92 ± 1.79	10.96 ± 3.02	< 0.01	0.086	< 0.01
K	70.82 ± 16.16	76.02 ± 15.89	0.253	0.072	0.368
Ca	0.21 ± 0.08	0.10 ± 0.03	< 0.01	-0.001	< 0.01
Mg	0.17 ± 0.02	0.14 ± 0.03	< 0.01	-0.000	< 0.01
Al	2.44 ± 0.30	5.47 ± 0.54	< 0.01	0.049	< 0.01
TEB	0.57 ± 0.05	0.43 ± 0.07	< 0.01	-0.002	< 0.01
OM	6.88 ± 1.14	14.30 ± 2.70	< 0.01	0.311	< 0.01

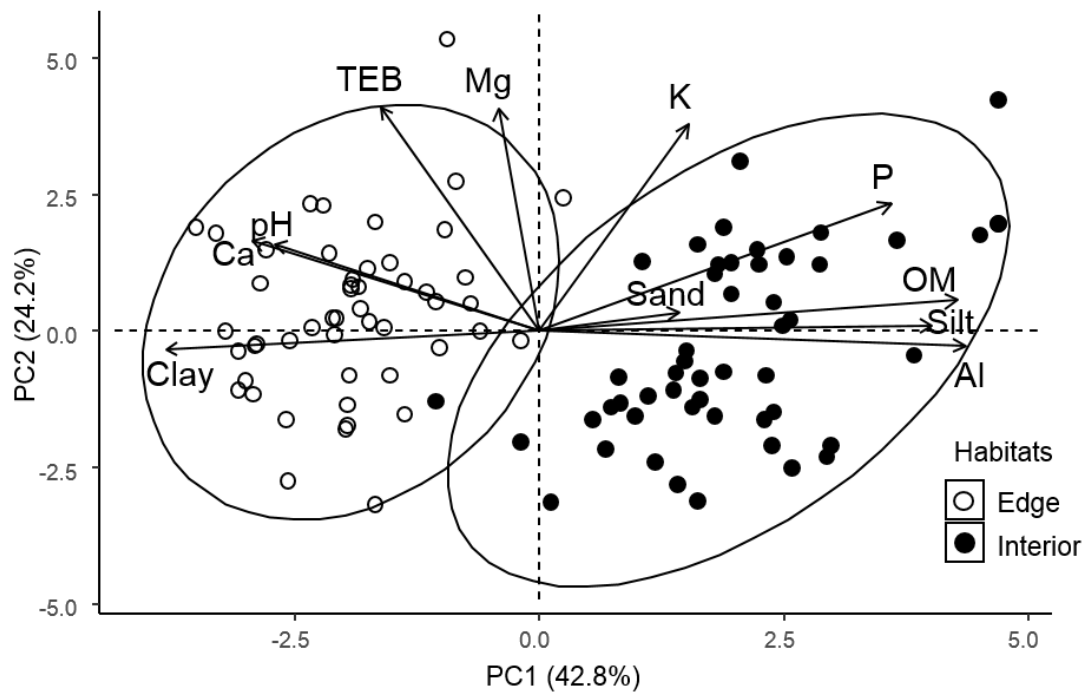


Figure 3: Principal Component Analysis (PCA) diagram showing the relationship between soil attributes and plots. Circles represent 95% of confidence interval. Abbreviations according to table 1.

Forest edge had significantly higher tree density and lower aboveground biomass (AGB), median tree height (Hmed), upper 95-percentile tree height (H95), and upper 95-percentile stem diameter (DBH95) than the forest interiors (Table 2, Fig. 4 a-f). Forest patch size and shape (higher values indicating more circular patches) were positively related to AGB, Hmed, and upper 95-percentile tree height (H95) (Table 2). When accounting for the effect of patch size and shape in the relationships between forest habitat and the structural community metrics (i.e. the interaction terms of models), tree density and upper 95-percentile stem diameter (DBH95) (marginally significant) tended to be higher in larger patches. In contrast, AGB and median stem diameter (DBHmed) were positively related to patch shape in forest interiors (Table 2, Fig. 5 a-d). These results indicate that besides differences between forest habitats, with increasing patch size and circularity, the forest interior has more biomass and taller trees with higher stem diameter compared to the forest edge.

Rarefied species richness and Fisher's diversity index were not significantly different between forest habitats. However, the interaction between forest habitat and patch size was marginally significant ($p = 0.09$) for species richness and significantly different for Fisher's diversity index in forest interior (Table 2, Fig. 5 e-f), indicating that with increasing patch size, species diversity is higher in the forest interior compared to the forest edge.

From the 107 sampled species, 61 (57%) were exclusive from each habitat (33 species in forest edge and 28 species in forest interiors). Species composition was significantly different between forest habitats, as illustrated by the nMDS ordination (Fig. 6) and confirmed by the PERMANOVA analysis. The SIMPER analysis identified the species that exhibit an increased contribution to the dissimilarity between the forest habitats (Appendix D). The nMDS axes 1 and 2 were significantly related to forest habitat, but not with patch size or shape (Appendix E).

Table 2: Results of model analyses used to evaluate differences in structure and diversity vs size and shape between forest edge and interior in patches of tropical montane cloud forests surrounded by native grasslands. Variables according to Figure 4.

Variables	Edge	Interior	Habitat	Size	Shape	Habitat x Size	Habitat x Shape
			p-value	p-value	p-value	p-value	p-value
Tree density	3235 ± 524	2260 ± 492	0.03	0.25	0.77	0.01	0.68
AGB	119.9 ± 40.5	254.7 ± 80.9	< 0.01	< 0.01	0.05	0.21	< 0.01
DBH _{median}	9.04 ± 1.54	10.92 ± 1.74	0.29	0.86	0.22	0.31	0.05
DBH ₉₅	22.13 ± 4.5	32.03 ± 6.5	< 0.01	0.87	0.4	0.07	0.84
H _{median}	6.84 ± 1.11	11.49 ± 2.41	< 0.01	< 0.01	< 0.01	0.36	0.24
H ₉₅	11.24 ± 1.69	17.1 ± 2.92	< 0.01	0.05	0.05	0.7	0.59
Srar	13.07 ± 1.69	13.59 ± 2.13	0.89	0.92	0.89	0.09	0.82
Fisher diversity	8.89 ± 2.65	10.05 ± 3.26	0.74	0.31	0.65	0.02	0.51

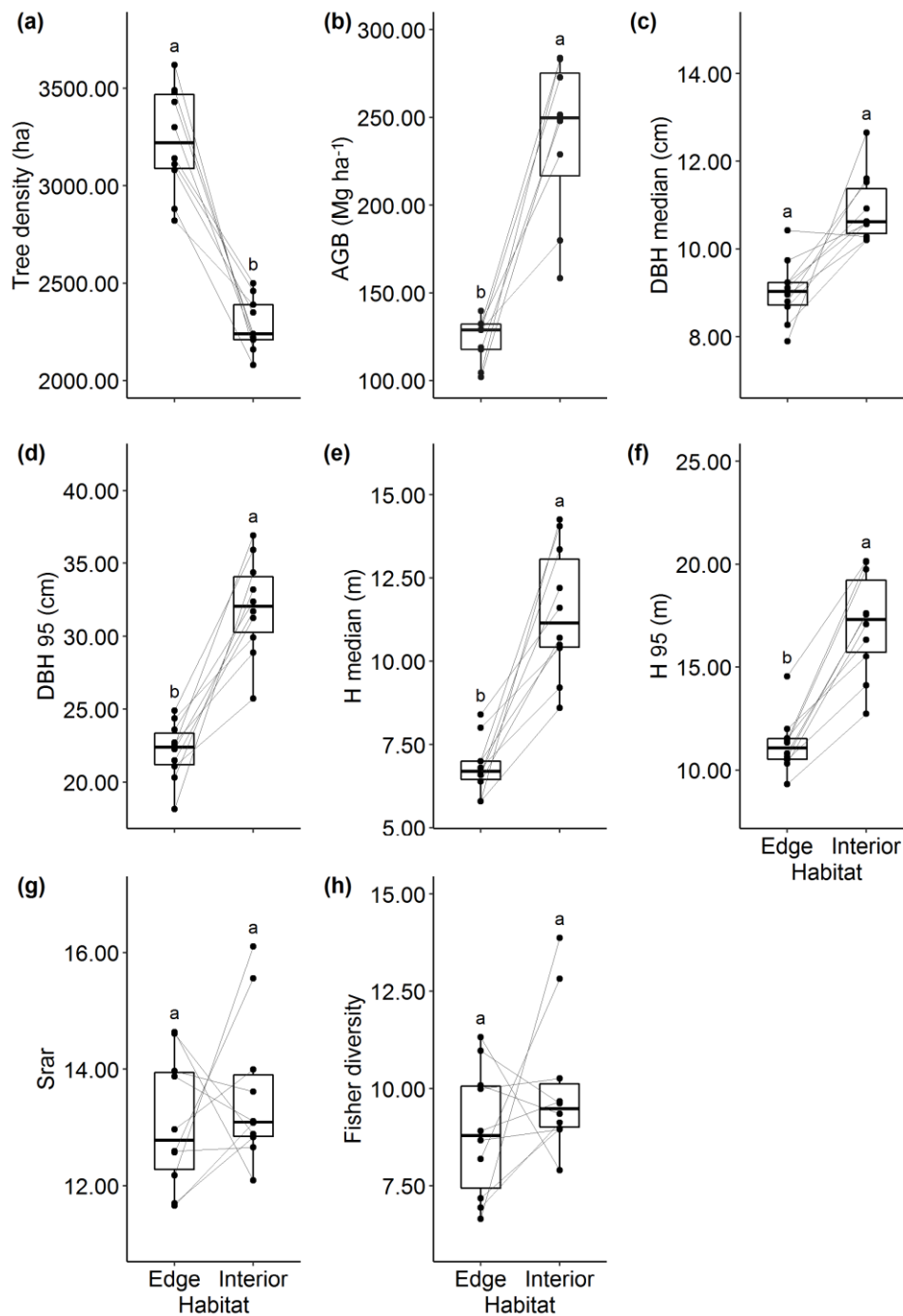


Figure 4: Comparison of structural and diversity species parameters between edge and interior habitats. Different lowercase letters above the boxes indicate significant ($p < 0.05$) differences. Lines represent comparisons of variables between habitats (edge and interior) of the same forest patch. AGB: aboveground biomass; DBH_{med} : median stem diameter; DBH_{95} : upper 95-percentile stem diameter; H_{med} : median tree height; H_{95} : upper 95-percentile tree height and Srar: rarefied species richness (random sampling of 29 trees).

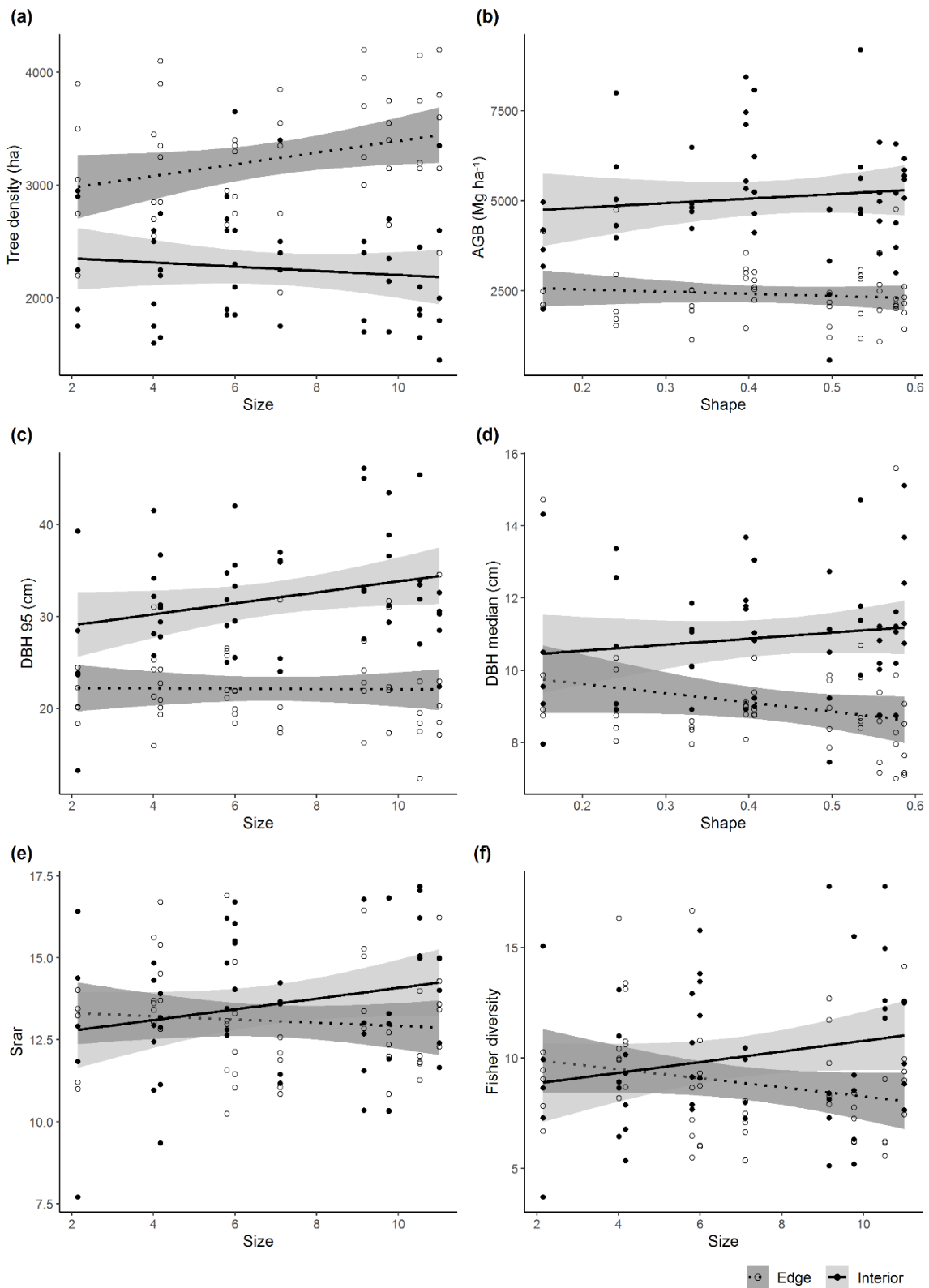


Figure 5: Comparison between structural parameters, species richness (Srar) and Fisher's diversity index with size and shape (higher values indicating more circular patches) of forest patches.

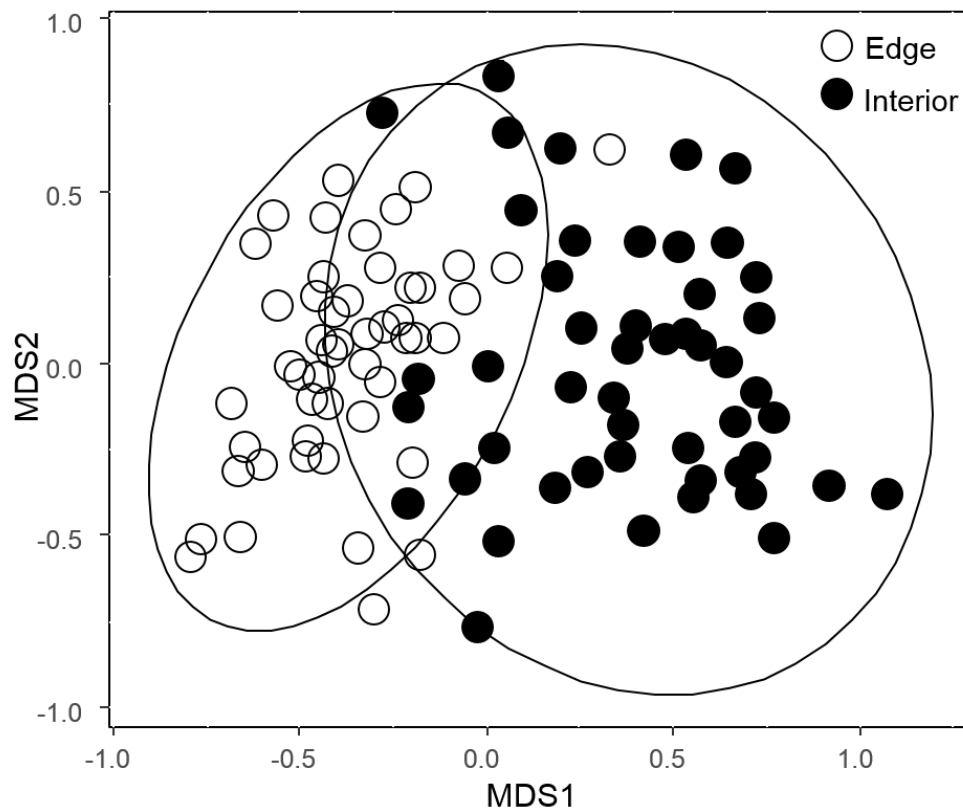


Figure 6: Nonmetric Multidimensional Scaling analysis (nMDS) showing the layout of the plots separated by edge and interior habitat. nMDS based on the Morisita-Horn similarity coefficient. Stress: 0.23. Circles represent 95% of confidence interval.

4. Discussion

We showed that edge habitat differs significantly from interior habitat for most community attributes in these natural and old forest patches surrounded by grasslands. Many of those differences were similar or even harsher than the ones found for recently created anthropogenic forest fragments. Therefore, possibly in recent fragmented patches, the differences between edge and interior must persist or even increase as the fragment ages, and the edge community adjusts itself to the new environmental conditions.

The decrease of the effect of external conditions (e.g. luminosity, temperature, and winds) further away from the edge was reflected directly in the structure and composition of species. The edge had smaller trees, lower biomass, and a predominance of light-demanding generalist species, while the interior had larger trees of shade-tolerant species, resulting in higher biomass. However, for these natural patches, differently from the artificially fragmented forest, soil attributes also contributed to a differentiation between edge and interiors.

In addition, we showed for the first time that patch size and shape are important drivers of community structure in natural patches. That is, small and less circular patches accumulate less biomass and have smaller individuals because they are subject to a greater edge effect. Although there are no differences in species richness among the studied habitats, in large patches, the richness was greater in the forest interior.

4.1. Edaphic variation

As we expected, organic matter accumulation was greater in the interior. With a gradual decrease in temperature (of the air and soil) and incidence of light in the forest interior (Magnago et al., 2015; van den Berg and Santos, 2003), microbial activities were lower, consequently, the rates of decomposition and mineralization decreased, resulting in higher organic matter content and a lower amount of exchangeable bases (Barreto-Garcia et al., 2019; Dalling et al., 2016). It is important to highlight that the regions of cloud forests are already colder places throughout the year compared to other forest formations, which further reduces microbial activities (Aparecido et al., 2018; Dalling et al., 2016; Roman et al., 2011). Moreover, micro-topographic variations between habitats may have contributed to differentiation, since soil organic matter can be transported along the slope by rain through

runoff, accumulating in the forest interior in the lower sections (Bot and Benites, 2005; Silva et al., 2007).

The decrease in pH and increase in available phosphorus in the interior-edge gradient are in line with several studies (Barreto-Garcia et al., 2019; Silva et al., 2019). With a greater accumulation of organic matter in the interior, there is also a greater release of humic acids related to soil acidification (Bolan et al., 2011; Ehrenfeld et al., 2005). In addition, increasing temperature near the edge decreases soil moisture, and acidity is correlated with moisture (Silva et al., 2019). The variation in phosphorus levels can be attributed to differences in pH because phosphorus retention and release in tropical forest soils are influenced by pH changes (Cerozi and Fitzsimmons, 2016; Sato and Comerford, 2005). However, phosphorus transportation by rain runoff to the lower sections cannot be dismissed (van den Berg and Santos, 2003).

In habitats with low pH, a higher concentration of aluminum was already expected, because, in acidic soils, aluminum becomes more soluble (Li and Johnson, 2016; Ritchie, 1995). Moreover, the high concentration of aluminum and low pH reduces the concentration of TEB in the interior (Hillel, 2005). Also, although not expected, the proportion of clay was higher at the edge, and this portion of the soil retains more cations because the particles are more aggregated and negatively charged (Bedel et al., 2018; Tahir and Marschner, 2016). Possibly, this higher proportion of clay at the edge was responsible for the higher concentration of Ca^{2+} and Mg^{2+} , resulting in higher TEB.

4.2. Community structure

Our prediction that the edge would have higher tree density composed of small-statured trees and lower aboveground biomass, compared to the forest interior due to the environmental differences (Coelho et al., 2016; Magnago et al., 2015), was confirmed. On

the edge, although the light availability is higher (van den Berg and Santos, 2003), the winds are more intense, there are greater variations in temperature and humidity (of air and soil) and fire events are more frequent (Magnago et al., 2015; Murcia, 1995; Silva et al., 2019; Wekesa et al., 2018). Under these conditions, even if the number of individuals increases, probably related to higher luminosity, mortality is higher and growth is lower (Bragion et al., 2018; Magnago et al., 2015), resulting in smaller individuals and less biomass (Erdős et al., 2018; Lippok et al., 2013; Silva et al., 2019).

In contrast, the forest interior has less variable environmental conditions (D'Angelo et al., 2004) with trees allocating resources to over compete with their neighbors, mainly in terms of access to light, reaching larger sizes (height and diameter), and resulting in larger biomass. Furthermore, the light gradient existent between the edge and forest interior deeply affects the species composition (van den Berg and Santos, 2003). The species occupying the edge are light-demanding, investing comparatively more in reproduction (more individuals) than growth with a short lifespan and reaching smaller sizes (Bragion et al., 2018; Gonzalez et al., 2010).

Lastly, as we expected, the size and shape of the patches were important drivers of the community structure. Edge and interior habitats differ more in terms of community attributes in large patches than in small ones. We found that as the patch size decreases and the irregularity of the shape increases, the forest interior becomes more similar to the edge, as a larger proportion of forest is affected by edge effects (Arellano-Rivas et al., 2018), in a similar way as in man-made forest fragments (Magnago et al., 2015; Murcia, 1995; Ries et al., 2004). On the other hand, the tree density was related to the size of the patch, with larger patches with fewer individuals (although larger) in the forest interior. With the reduction of the edge effect, trees allocate more resources in diameter growth, therefore, large individuals are found in large forest patches (Erdős et al., 2018; Murcia, 1995).

Our data show that even in forest patches with a natural matrix, the shape and size of the patch are important metrics to infer the community structure. Furthermore, the edge effect seems to be something rather permanent on forest patches, either natural or man-made.

4.3. Richness and Species composition

We predicted that the richness and diversity of species in the interior would be larger than at the edge, but we found this pattern only for the larger patches. The edges are areas of transition from a forest habitat to grasslands and, therefore, can be understood as ecotonal habitats (Kark, 2007; Ries et al., 2004). Ecotones can have high diversity because of the mutual contribution of neighboring communities (Gonzalez et al., 2010; Murcia, 1995; Ries et al., 2004; Williams-Linera, 1990). On the other hand, we found a pervasive edge effect for the small patches (*sensu* Murcia, 1995), reducing the differentiation between edge and interior, contributing to similar species diversity. In large patches, instead, the proportion of the patch area affected by the edge effect is smaller and the absolute size of forest core increases, allowing the occurrence of more specialized species (Murcia, 1995; Rogan and Lacher, 2018), and resulting in a possibly higher diversity in the interior. We were already expecting greater diversity in the interior due to the great spatial heterogeneity of this habitat, in contrast to the edge that presents strong environmental filters and similar abiotic restrictions throughout (Ries et al., 2004).

Moreover, environmental conditions of edge vary to a lesser extent among the plots because they were all placed where the forest meets the grassland. In contrast, the interior habitat plots were randomly allocated 20 meters from the edge to the core of the patch, resulting in higher microenvironment variation. In addition, Ribeiro (unpublished data) comparing plots of interior of the present study found great heterogeneity in edaphic conditions between forest patches. This higher environmental heterogeneity possibly affects

the species composition (Dalling et al., 2016; Neri et al., 2012) and increases diversity in the interior.

As we expected, species composition showed marked differences between habitats. The edge have a higher luminous intensity and air temperature, and drier soils than the interior (Erdős et al., 2019; Magnago et al., 2015; van den Berg and Santos, 2003). Also, some studies have shown that differences in species composition between the edge and interior habitats are related to changes in soil nutrients (Terra et al., 2018; van den Berg and Oliveira-Filho, 1999; Wekesa et al., 2018). Therefore, contrasting conditions between the edge and interior work as environmental filters, selecting species, and differentiating the habitats in terms of species composition (Kraft et al., 2015; Laliberte et al., 2014).

Because light and soil moisture are the most important variables on the differentiation between edge and interior of natural patches (van den Berg and Santos, 2003). In the interior, the light penetration occurs exclusively throughout the canopy, which is high and multilayered, reducing, even more, the available light to the understory and regenerating stratum (Kabakoff and Chazdon, 1996).

5. Conclusions

Our study showed that classical human-driven edge effects also hold for forest patches with natural edges. Our results show natural edges composed by small-statured trees and lower aboveground biomass compared to forest interiors, in addition to significant differences in species composition between both habitats. We found significant evidence that patches shape and size are important drivers of structure and tree diversity. Moreover, soil characteristics in these natural patches also differed between interior and edge habitat, contributing potentially to differentiation between these habitats.

As for man-made fragments, our results also showed that the peculiarities of each habitat, as well as the size and shape of natural patches, must be taken into account for conservation and management decisions. To support those decisions, other studies that include the functional diversity and dynamics of these forest patches are necessary.

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Supplementary Material

Appendix A: Location of 10 patches of Tropical Montane Cloud Forests (TMCF) (Minas Gerais State, Brazil) with their geographic coordinates, altitude and size.

Forest patch	Latitude	Longitude	Altitude (m)	Area (ha)
1	22° 7'26.82"S	44°44'8.50"W	1955	10.5
2	22° 7'9.60"S	44°44'12.42"W	1933	6.8
3	22° 7'6.11"S	44°44'25.86"W	1885	5.6
4	22° 7'26.18"S	44°44'42.37"W	1910	9.8
5	22° 7'39.71"S	44°44'19.35"W	1970	5.8
6	22° 7'20.74"S	44°45'40.55"W	1896	4.2
7	22° 7'23.17"S	44°45'56.02"W	1908	9.2
8	22° 7'40.07"S	44°45'19.06"W	1879	11
9	22° 7'43.15"S	44°44'58.76"W	1925	3.9
10	22° 7'54.03"S	44°44'59.52"W	1933	2.1

Appendix B: Tree species parameters, in edge and interior habitats, in cloud forest patches of the Serra do Papagaio State Park – Minas Gerais State, Brazil. Species ordered according to the IV of edge habitat. Acronyms: AD – absolute density (ind.ha⁻¹); BA – basal area (m².ha⁻¹); NC - number of forest patches in which the species were sampled; IV – importance value (%).

Family	Species	Edge				Interior			
		AD	BA	NP	IV (%)	AD	BA	NP	IV (%)
Myrtaceae	<i>Myrceugenia bracteosa</i> (DC.) D.Legrand & Kausel	466	6.517	10	12.182	158	6.054	10	7.891
Myrtaceae	<i>Myrcia retorta</i> Cambess.	255	6.961	10	10.315	276	14.304	10	15.179
Myrtaceae	<i>Siphoneugena crassifolia</i> (DC.) Proença & Sobral	379	5.037	10	9.948	80	0.892	10	3.163
Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.	331	1.752	10	6.681	145	1.187	10	4.634
Myrtaceae	<i>Myrcia subcordata</i> DC.	208	2.471	10	5.812	104	2.539	10	4.488
Primulaceae	<i>Myrsine gardneriana</i> A.DC.	184	2.038	10	5.230	41	0.853	9	1.957
Rubiaceae	<i>Psychotria vellosiana</i> Benth.	162	1.702	10	4.535	49	0.704	10	2.182
Rubiaceae	<i>Cordia concolor</i> (Cham.) Kuntze	160	0.554	10	3.606	75	0.408	10	2.781
Myrtaceae	<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	112	1.216	10	3.352	195	2.430	10	6.084
Proteaceae	<i>Roupala montana</i> Aubl.	91	1.276	10	3.295	27	1.355	9	1.990
Malpighiaceae	<i>Byrsonima ligustrifolia</i> A.Juss.	54	1.518	10	2.795	65	1.538	9	2.991
Aquifoliaceae	<i>Ilex microdonta</i> Reissek	75	0.863	8	2.379	100	3.439	10	5.326
Symplocaceae	<i>Symplocos falcata</i> Brand	85	0.569	10	2.303	1	0.008	1	0.060
Monimiaceae	<i>Macropeplus dentatus</i> (Perkins) I.Santos & Peixoto	50	0.357	10	1.870	11	0.200	6	0.573
Asteraceae	<i>Vernonanthura discolor</i> (Spreng.) H.Rob.	38	0.735	9	1.853	11	0.372	7	0.804
Primulaceae	<i>Myrsine umbellata</i> Mart.	49	0.225	10	1.675	29	0.386	8	1.240
Asteraceae	<i>Piptocarpha regnellii</i> (Sch.Bip.) Cabrera	25	0.533	7	1.328	-	-	-	-
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	32	0.245	9	1.299	27	0.258	9	1.411
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	30	0.214	9	1.252	-	-	-	-
Lauraceae	<i>Ocotea pulchella</i> (Nees & Mart.) Mez	34	0.347	7	1.190	24	0.407	9	1.220

Clethraceae	<i>Clethra scabra</i> Pers.	27	0.495	8	1.172	10	0.368	7	0.786
Myrtaceae	<i>Myrceugenia miersiana</i> (Gardner) D.Legrand & Kausel	28	0.161	6	1.006	-	-	-	-
Meliaceae	<i>Cabralea canjerana</i> (Vell.) Mart.	23	0.249	7	0.993	31	1.147	9	1.957
Celastraceae	<i>Monteverdia gonoclada</i> (Mart.) Biral	24	0.158	9	0.889	36	1.379	7	2.057
Euphorbiaceae	<i>Croton alchorneicarpus</i> Croizat	24	0.104	6	0.879	7	0.077	5	0.354
Melastomataceae	<i>Miconia budlejoides</i> Triana	23	0.063	6	0.798	6	0.036	4	0.273
Asteraceae	<i>Baccharis oreophila</i> Malme	19	0.168	7	0.701	-	-	-	-
Myrtaceae	<i>Myrceugenia regnelliana</i> (O.Berg) D.Legrand & Kausel	24	0.104	7	0.698	31	0.159	4	0.842
Aquifoliaceae	<i>Ilex theezans</i> Mart. ex Reissek	12	0.242	6	0.656	-	-	-	-
Myrtaceae	<i>Myrcia laruotteana</i> Cambess.	14	0.073	7	0.532	20	0.409	3	0.717
Winteraceae	<i>Drimys brasiliensis</i> Miers	17	0.153	4	0.487	44	0.454	10	1.787
Symplocaceae	<i>Symplocos revoluta</i> Casar.	11	0.125	1	0.473	17	0.343	6	0.833
Melastomataceae	<i>Miconia pusilliflora</i> (DC.) Naudin	13	0.041	6	0.458	277	1.249	10	6.579
Euphorbiaceae	<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	12	0.093	2	0.420	18	0.315	6	0.830
Asteraceae	<i>Eremanthus erythropappus</i> (DC.) MacLeish	8	0.165	3	0.404	-	-	-	-
Araliaceae	<i>Schefflera calva</i> (Cham.) Frodin & Fiaschi	8	0.056	3	0.384	15	0.372	3	0.701
Podocarpaceae	<i>Podocarpus lambertii</i> Klotzsch ex Endl.	8	0.112	3	0.359	4	0.169	3	0.328
Lauraceae	<i>Ocotea corymbosa</i> (Meisn.) Mez	6	0.091	4	0.357	51	1.361	9	2.752
Myrtaceae	<i>Pimenta pseudocaryophyllus</i> (Gomes) Landrum	7	0.048	4	0.331	19	0.132	8	0.809
Myrtaceae	<i>Myrcia venulosa</i> DC.	7	0.113	4	0.314	23	0.313	7	1.024
Ochnaceae	<i>Ouratea</i> cf. <i>semiserrata</i> (Mart. & Nees) Engl.	7	0.066	4	0.310	-	-	-	-
Symplocaceae	<i>Symplocos insignis</i> Brand	6	0.078	2	0.310	8	0.128	4	0.402
Primulaceae	<i>Myrsine lancifolia</i> Mart.	5	0.029	5	0.257	4	0.025	2	0.156
Aquifoliaceae	<i>Ilex</i> sp1	6	0.043	3	0.244	-	-	-	-
Myrtaceae	<i>Myrcia montana</i> Cambess.	4	0.057	2	0.235	-	-	-	-
Rhamnaceae	<i>Frangula sphaerosperma</i> (Sw.) Kartesz & Gandhi	5	0.021	3	0.214	2	0.011	2	0.117
Melastomataceae	<i>Huberia nettoana</i> Brade	5	0.040	2	0.194	3	0.007	2	0.129
Myrtaceae	<i>Myrceugenia</i> cf. <i>rufescens</i> (DC.) D.Legrand & Kausel	3	0.048	2	0.180	5	0.163	3	0.339

Apocynaceae	<i>Aspidosperma olivaceum</i> Müll.Arg.	3	0.046	3	0.179	-	-	-	-
Myrtaceae	<i>Siphoneugena cf. densiflora</i> O.Berg	3	0.020	3	0.157	-	-	-	-
Asteraceae	<i>Piptocarpha axillaris</i> (Less.) Baker	4	0.048	2	0.155	-	-	-	-
Asteraceae	<i>Vernonanthura</i> sp2	2	0.113	1	0.154	-	-	-	-
Myrtaceae	<i>Myrcia guianensis</i> (Aubl.) DC.	6	0.022	2	0.153	-	-	-	-
Asteraceae	<i>Austrocritonia velutina</i> (Gardner) R.M.King & H.Rob.	3	0.011	3	0.149	-	-	-	-
Symplocaceae	<i>Symplocos</i> sp1	3	0.085	1	0.140	-	-	-	-
Melastomataceae	<i>Leandra aurea</i> (Cham.) Cogn.	4	0.021	3	0.131	-	-	-	-
Lauraceae	Lauraceae sp1	2	0.037	2	0.125	-	-	-	-
Melastomataceae	<i>Miconia sellowiana</i> Naudin	2	0.023	1	0.113	12	0.086	6	0.515
Myrtaceae	<i>Eugenia widgrenii</i> Sond. ex O.Berg	2	0.017	1	0.108	48	1.191	7	2.155
Asteraceae	<i>Vernonanthura</i> sp1	2	0.058	1	0.106	-	-	-	-
Lauraceae	Lauraceae sp2	2	0.011	1	0.103	2	0.014	1	0.079
Primulaceae	<i>Myrsine</i> sp1	2	0.010	2	0.102	-	-	-	-
Myrtaceae	Myrtaceae sp1	2	0.005	2	0.097	-	-	-	-
Araucariaceae	<i>Araucaria angustifolia</i> (Bertol.) Kuntze	2	0.024	1	0.077	7	1.220	3	1.165
Lauraceae	Lauraceae sp3	1	0.027	1	0.069	-	-	-	-
Asteraceae	<i>Vernonanthura</i> sp3	1	0.025	1	0.068	-	-	-	-
Vochysiaceae	<i>Vochysia magnifica</i> Warm.	1	0.017	1	0.061	-	-	-	-
Myrtaceae	<i>Myrceugenia cf. campestris</i> (DC.) D.Legrand & Kausel	1	0.011	1	0.056	-	-	-	-
Lauraceae	<i>Ocotea nitida</i> (Meisn.) Rohwer	1	0.009	1	0.054	-	-	-	-
Thymelaeaceae	<i>Daphnopsis</i> sp	1	0.005	1	0.051	-	-	-	-
Lauraceae	<i>Nectandra grandiflora</i> Nees	1	0.004	1	0.050	17	0.635	7	1.060
Aquifoliaceae	<i>Ilex</i> sp2	1	0.003	1	0.049	2	0.100	1	0.174
Symplocaceae	<i>Symplocos celastrinea</i> Mart.	1	0.003	1	0.049	-	-	-	-
Rubiaceae	<i>Psychotria</i> sp1	1	0.003	1	0.049	-	-	-	-
Melastomataceae	<i>Miconia theizans</i> (Bonpl.) Cogn.	1	0.002	1	0.048	-	-	-	-
Asteraceae	Asteraceae sp1	1	0.002	1	0.048	-	-	-	-

Aquifoliaceae	<i>Ilex chamaedryfolia</i> Reissek	1	0.002	1	0.048	-	-	-	-
Asteraceae	<i>Piptocarpha macropoda</i> (DC.) Baker	1	0.002	1	0.048	-	-	-	-
Undetermined	Undetermined 1	1	0.002	1	0.048	7	0.106	2	0.252
Undetermined	Undetermined	-	-	-	-	36	1.046	10	2.128
Bignoniaceae	<i>Jacaranda cuspidifolia</i> Mart.	-	-	-	-	7	0.458	5	0.638
Melastomataceae	<i>Leandra carassana</i> (DC.) Cogn.	-	-	-	-	8	0.107	4	0.429
Lauraceae	<i>Ocotea odorifera</i> (Vell.) Rohwer	-	-	-	-	6	0.246	2	0.407
Monimiaceae	<i>Mollinedia</i> sp.	-	-	-	-	6	0.068	3	0.334
Melastomataceae	<i>Miconia</i> cf. <i>acutifolia</i> Ule	-	-	-	-	10	0.041	2	0.254
Melastomataceae	<i>Miconia latecrenata</i> (DC.) Naudin	-	-	-	-	7	0.040	2	0.250
Cunoniaceae	<i>Weinmannia paulliniifolia</i> Pohl ex Ser.	-	-	-	-	3	0.190	2	0.246
Undetermined	Undetermined 2	-	-	-	-	2	0.208	1	0.243
Ochnaceae	<i>Ouratea</i> sp2	-	-	-	-	4	0.023	3	0.235
Cunoniaceae	<i>Lamanonia ternata</i> Vell.	-	-	-	-	2	0.106	2	0.178
Ochnaceae	<i>Ouratea</i> sp1	-	-	-	-	2	0.072	2	0.157
Annonaceae	<i>Annona rugulosa</i> (Schltdl.) H.Rainer	-	-	-	-	3	0.015	2	0.135
Undetermined	Undetermined 3	-	-	-	-	2	0.017	2	0.121
Undetermined	Undetermined 9	-	-	-	-	2	0.008	2	0.116
Rubiaceae	<i>Rudgea jasminoides</i> (Cham.) Müll.Arg.	-	-	-	-	2	0.005	2	0.113
Celastraceae	<i>Monteverdia evonymoides</i> (Reissek) Biral	-	-	-	-	2	0.056	1	0.106
Undetermined	Undetermined 8	-	-	-	-	1	0.050	1	0.087
Melastomataceae	<i>Eugenia handroana</i> D.Legrand	-	-	-	-	2	0.020	1	0.083
Annonaceae	<i>Guatteria</i> sp1	-	-	-	-	1	0.038	1	0.079
Annonaceae	<i>Guatteria australis</i> A.St.-Hil.	-	-	-	-	1	0.030	1	0.074
Fabaceae	<i>Dalbergia villosa</i> (Benth.) Benth.	-	-	-	-	1	0.024	1	0.070
Dicksoniaceae	<i>Dicksonia sellowiana</i> Hook.	-	-	-	-	1	0.021	1	0.069
Theaceae	<i>Laplacea fruticosa</i> (Schrad.) Kobuski	-	-	-	-	1	0.014	1	0.064
Cyatheaceae	<i>Alsophila setosa</i> Kaulf.	-	-	-	-	1	0.010	1	0.061

Undetermined	Undetermined 7	-	-	-	-	1	0.007	1	0.059
Solanaceae	<i>Solanum capoerum</i> Dunal	-	-	-	-	1	0.006	1	0.059
Solanaceae	<i>Solanum swartzianum</i> Roem. & Schult.	-	-	-	-	1	0.003	1	0.057

Appendix C: Principal component analysis (PCA) results with eigenvalues of the first two axes in relation to the values of soil variables analyzed in the 100 plots of the forest patches.

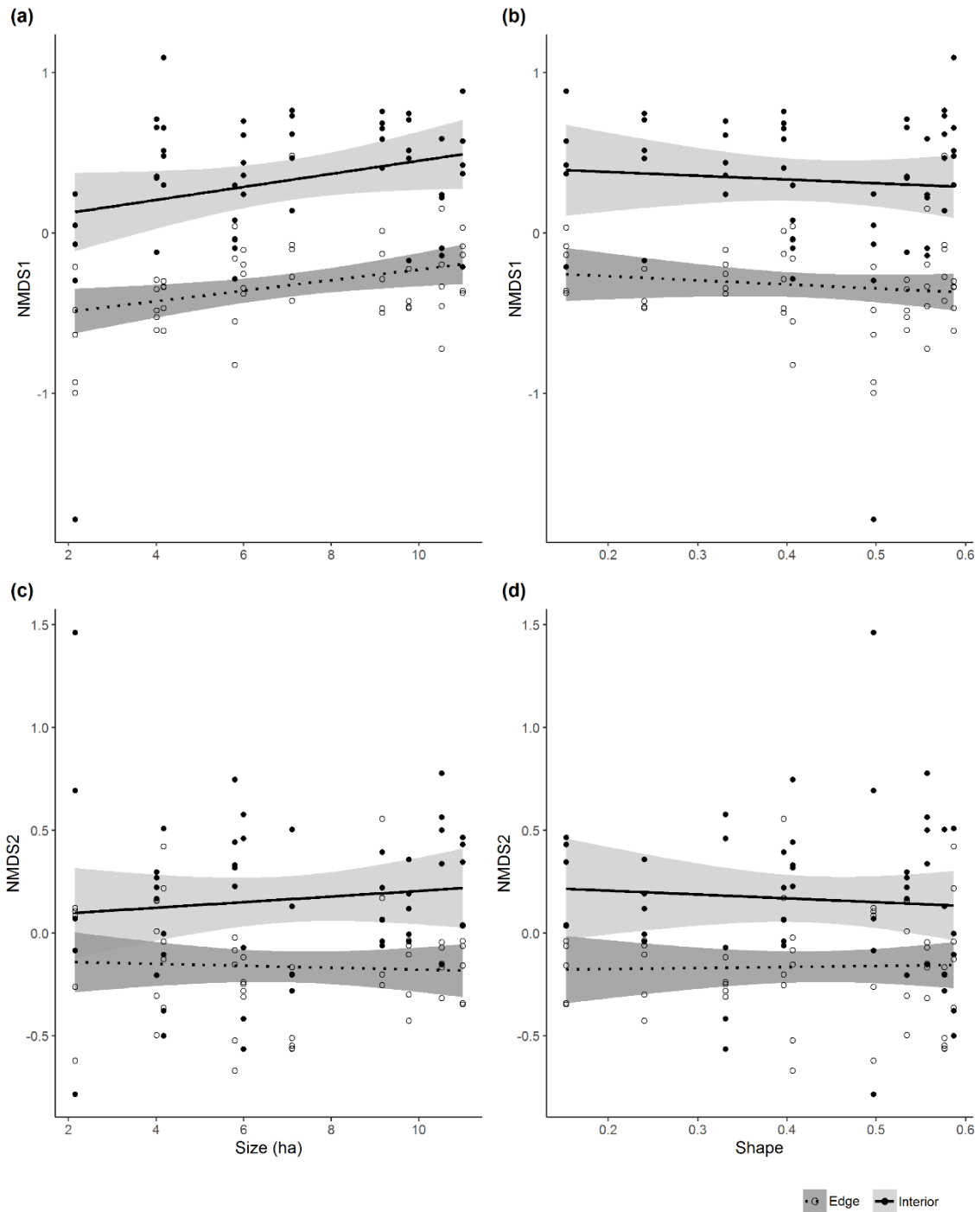
In addition, correlation coefficients of the same soil variables with the first two axes. r^2 = coefficient of determination.

	PC1	PC2
Eigenvalue	4.71	2.66
Proportion Explained	0.4278	0.2421
Cumulative Proportion	0.4278	0.6699
Soil variables		
Clay	-0.8142	-0.0714
Silt	0.8529	0.0223
Sand	0.3053	0.0733
pH	-0.5752	0.3413
P	0.7641	0.4958
K	0.3245	0.8017
Ca	-0.6251	0.3516
Mg	-0.0912	0.8634
Al	0.9255	-0.0546
TEB	-0.3468	0.8717
OM	0.9088	0.1201

Appendix D: SIMPER (Similarity Percentages) analysis for the 18 most abundant tree sampled species and their relative contribution to the dissimilarity in species composition between the forests edge and interior. Contribution = species percentage contribution to the dissimilarity; Cumulative = cumulative dissimilarity contribution; Forest habitat = average species abundance in forest edge and interior; p-value = permutation p-value (gray shaded numbers indicate significant differences in relative abundance, considering an alpha of 0.05).

Species	Contribution	Cumulative	Forest habitat		p-value
			Edge	Interior	
<i>Miconia pusilliflora</i>	0.06	0.11	0.41	12.35	0.001
<i>Siphoneugena crassifolia</i>	0.04	0.19	11.77	3.48	0.001
<i>Myrceugenia bracteosa</i>	0.04	0.27	14.57	7.11	0.001
<i>Myrciaria floribunda</i>	0.03	0.32	3.44	8.62	0.007
<i>Myrcia retorta</i>	0.03	0.37	7.90	12.24	0.054
<i>Myrcia splendens</i>	0.03	0.42	10.25	6.41	0.033
<i>Myrcia subcordata</i>	0.02	0.46	6.40	4.67	0.350
<i>Myrsine gardneriana</i>	0.02	0.50	5.65	1.82	0.001
<i>Psychotria vellosiana</i>	0.02	0.53	4.97	2.13	0.045
<i>Ilex microdonta</i>	0.01	0.56	2.22	4.58	0.019
<i>Symplocos falcata</i>	0.01	0.58	2.67	0.04	0.001
<i>Cordia concolor</i>	0.01	0.61	4.94	3.30	0.020
<i>Ocotea corymbosa</i>	0.01	0.63	0.19	2.32	0.002
<i>Byrsonima ligustrifolia</i>	0.01	0.65	1.58	2.84	0.133
<i>Eugenia widgrenii</i>	0.01	0.67	0.07	2.10	0.004
<i>Roupala montana</i>	0.01	0.68	2.82	1.18	0.040
<i>Drimys brasiliensis</i>	0.01	0.70	0.53	2.08	0.017
<i>Myrceugenia regnelliana</i>	0.01	0.72	0.73	1.38	0.309

Appendix E: Comparison of nMDS axes (nMDS1 and nMDS2) with size and shape (higher values indicating more circular patches) of forest patches.



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ARTIGO 2

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**Intraspecific trait variation shows that functional diversity
decreases in natural forest edges compared to forest interiors**

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11 Lucas Deziderio Santana, Jamir A. Prado-Junior, José Hugo C. Ribeiro, Kelly M. G.

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17 **Artigo formatado de acordo com as normas da revista Functional Ecology**

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24 **Intraspecific trait variation shows that functional diversity decreases in natural**
25 **forest edges compared to forest interiors**

26 **Abstract**

27 **1.** Plant species can have different functional traits to respond the habitats with contrasting
28 environmental conditions and resources, and intraspecific trait variation can increase the
29 chances of successful establishment of organisms in these locations. Here, we explored
30 how forest edges and interiors differ in traits and functional diversity and if the habitats
31 to drive variations in traits values of co-occurring species. In addition, we assessed how
32 the inclusion of intraspecific trait variation (ITV) can affect the assessment of functional
33 metrics from nearby, but contrasting, habitats.

34 **2.** Our dataset covers a 2-ha sampling effort (1 ha for each forest habitat) distributed
35 across ten tropical montane cloud forest (TMCF) patches surrounded by native
36 grasslands. In each patch, we established five plots right on the edge and five randomly
37 distributed over the forest interior and collected functional traits (leaf, allometric and
38 wood density) for all species that reached five individuals or more (edge and forest
39 interior separately) in each habitat, totaling a dataset with 5418 trees distributed in 62
40 species, which 33 species were sampled in both habitats. We assessed the functional
41 diversity using functional richness (FRic), divergence (FDiv) and dispersion (FDis). And
42 to test the impact of using the intraspecific variation to compare trait values and functional
43 diversity indices we set up two scenarios: one excluding intraspecific variation (using the
44 mean values of species traits) and another including intraspecific variation (sampled
45 multiple individuals of each species across all sites).

46 **3.** We found that the edge and interior have individuals with distinct functional traits,
47 however, that alleviate the inherent stress of each habitat. The edge was also proved to be

48 a more selective habitat in terms of range of functional traits, which reflected in less
49 functional diversity. We showed that habitats play an important role on ITV values and
50 that the statistically significant differences between habitats, in relation to traits and
51 functional diversity, were better observed with the inclusion of intraspecific variation.

52 **4.** Our study shows the potential of using natural forest patches to understand the edge
53 effect, regardless of habitat loss. In addition, we highlight the importance of incorporating
54 ITV in functional diversity studies, especially those on a smaller scale and that
55 incorporate quantitative variables, to better understand and predict ecological patterns.

56 **Key-words:** allometric traits, cloud forest, edge-interior gradient, ITV, leaf traits, plant
57 functional traits

58

59 **1. Introduction**

60 Functional traits are associated with the growth, reproduction and survival of
61 individuals (Violle et al., 2007) and their use is growing around the world as a tool to
62 understand how the characteristics of a group of species drive the functioning of the
63 ecosystem (Diaz et al., 2004; Poorter et al., 2008; Prado-Junior et al., 2016; Toledo-
64 Aceves et al., 2019; Wright et al., 2010). This growth resulted in the creation of several
65 databases of functional traits (Chave et al., 2009; Fraser, 2020) which have been applied
66 in the most varied contexts: productivity and resilience of communities (Bernhardt-
67 Römermann et al., 2011; Šímová et al., 2019; Staples et al., 2019), biological interactions
68 (Haase et al., 2015), climate change (Wieczynski et al., 2018), land use (Pyles et al., 2020)
69 and in the scope of conservation (Pelletier et al., 2018).

70 Some studies have pointed out that the traits are conserved phylogenetically
71 (Chave et al., 2006; Hoffmann & Franco, 2008; Webb et al., 2002), so the use of

72 taxonomical levels above species to calculate a respective trait may be an alternative in
73 the absence of data (Chave et al., 2006). However, in contrast to the widespread use of
74 data at the most varied taxonomic levels, there is no doubt that functional traits vary
75 among conspecific individuals (Albert et al., 2011; Siefert et al., 2015), and that the
76 inclusion of this intraspecific variation will sharp our comprehension about patterns and
77 processes of biological communities (Albert et al., 2012; Cianciaruso et al., 2009; Umaña
78 & Swenson, 2019; Vergara-Gómez et al., 2019). The phenotypic variation, either based
79 on genetic variation or phenotypic plasticity, reflects the ability of species to respond to
80 filters and biological interactions (Hulshof & Swenson, 2010; Jung et al., 2010; Pritzkow
81 et al., 2019; Toledo-Aceves et al., 2019).

82 The traits' phenotypic variation, reflecting plant physiology, morphology and
83 reproduction, can increase the chances of successful establishment of organisms in
84 locations with variable conditions (Toledo-Aceves et al., 2019; Valladares et al. 2007,
85 2014). In addition, some studies have shown that the amplitude of phenotypic changes is
86 linked to the intensity of the environmental filter (Barros et al., 2012; Jung et al., 2010),
87 from this perspective, the environment is seen as a selective force, excluding individuals
88 unable to tolerate conditions at a particular location (Jung et al., 2010; Kraft et al., 2015).
89 Thus, understanding the role of phenotypic variation of functional traits in diverging
90 habitats is important to understand the main ecological processes that taking place in
91 communities directing their structure and dynamics (Albert et al., 2011; Chalmandrier et
92 al., 2017; Siefert et al., 2015).

93 The forests' edge and interior are contrasting habitats in terms of environmental
94 conditions and resources (Casenave et al., 1995; Coelho et al., 2016; Kolodziejek, 2014),
95 and useful models to understand the adaptation of species in response to those differences.
96 In forest patches with natural edges, the edge and interior habitats are long ago established

97 and more or less stable (Bragion et al., 2018; Coelho et al., 2018; Hoffmann et al., 2012).
98 In these systems, the strength of stressful factors generally decreases from the edge to
99 the interior, which can also be called the edge effect (Bragion et al., 2018; Guimarães et
100 al., 2008; Santana et al., 2021). Forest edges have higher light incidence, with a
101 consequent increase in the temperature of both the air and the soil, greater exposure to
102 winds, reduced water supply in the soil, higher seasonal and diurnal variation of climate
103 conditions, and greater vulnerability to fire events (Coelho et al., 2016; D'Angelo et al.,
104 2004; Magnago et al., 2015). In addition, forest patches in montane ecosystems are also
105 subject to frost (Aparecido et al., 2018; Dreyer et al., 2020) and their forest edges for
106 being in direct contact with open landscape (savanna) are the most affected (Hoffmann et
107 al., 2019). In contrast, forest interior, besides being more stable environments (D'Angelo
108 et al., 2004; Guimarães et al., 2008), have lower light incidence (van den Berg & Santos,
109 2003), favoring organisms with conservative strategies, such as low rates of
110 photosynthesis and respiration, slow growth and higher survival (Weemstra et al., 2016).
111 However, this pattern of resource-use and -acquisition can be changed in some functional
112 traits of habitats with strong environmental filters (Asefa et al., 2017; Reich, 2014; Wright
113 et al., 2004), as has been shown in some studies (Borges et al., 2018; Silva et al., 2019).
114 Thus, conservative strategy would increase plant's stress-tolerance (Verbeek et al., 2019;
115 Wright et al., 2004), such as at the edges.

116 In view of the differences between forest edge and interior, functional diversity
117 becomes an important tool to try to understand the main ecological processes that drive
118 species occupation and community structure in each habitat (Cianciaruso et al., 2009;
119 Mouchet et al., 2010). Habitats with strong environmental filters, for example, tend to
120 show convergence in the functional traits, consequently, lower functional diversity
121 (Götzenberger et al., 2012; Mouchet et al., 2010). However, despite the current

122 understanding of the importance of intraspecific variation in functional studies, none of
123 the methods for estimating functional diversity provides a clear way to incorporate this
124 level of variation (Albert et al., 2012; Petchey & Gaston, 2006). Most methods use the
125 average values of species traits, although the species in each habitat can express different
126 phenotypes and play a different roles in the functioning of community (Pérez-Ramos et
127 al., 2019; Siefert et al., 2015; Umaña & Swenson, 2019).

128 In this study, we evaluated how forest edges and interiors differ in traits and
129 functional diversity and how the inclusion of intraspecific trait variation affects the
130 assessment of the functional diversity in those habitats. We present functional traits data
131 of ten natural tropical montane cloud forest patches surrounded by grasslands, and
132 address the following hypotheses: (i) Considering that natural forest patches are also
133 affected by the edge effect (Santana et al., 2021), we expect that individuals in edge have
134 functional traits related to the reduction of stress caused by these conditions (lower leaf
135 area and specific leaf area, higher leaf thickness, shorter petiole, shallower crown, smaller
136 diameter and higher wood density). In contrast, forest interior would have the opposite
137 pattern conditioned by the need of intercept and use the low available light in this shaded
138 habitat. We also expect that the edge to have less functional diversity because it has
139 stronger environmental filters and consequently less variation in functional traits. (ii)
140 Considering that the functional traits can vary at the individual level (Siefert et al., 2015)
141 we expect that the contrasting habitats (edge and interior) **to drive variations in traits**
142 **values of co-occurring species.** (iii) Finally, we expect that the sampling strategy with
143 **inclusion of intraspecific variation at the habitat level to show stronger and more**
144 **significant relationships between contrasting forest habitats (increase the models'**
145 **explanatory capabilities) than using the mean values of species traits.**

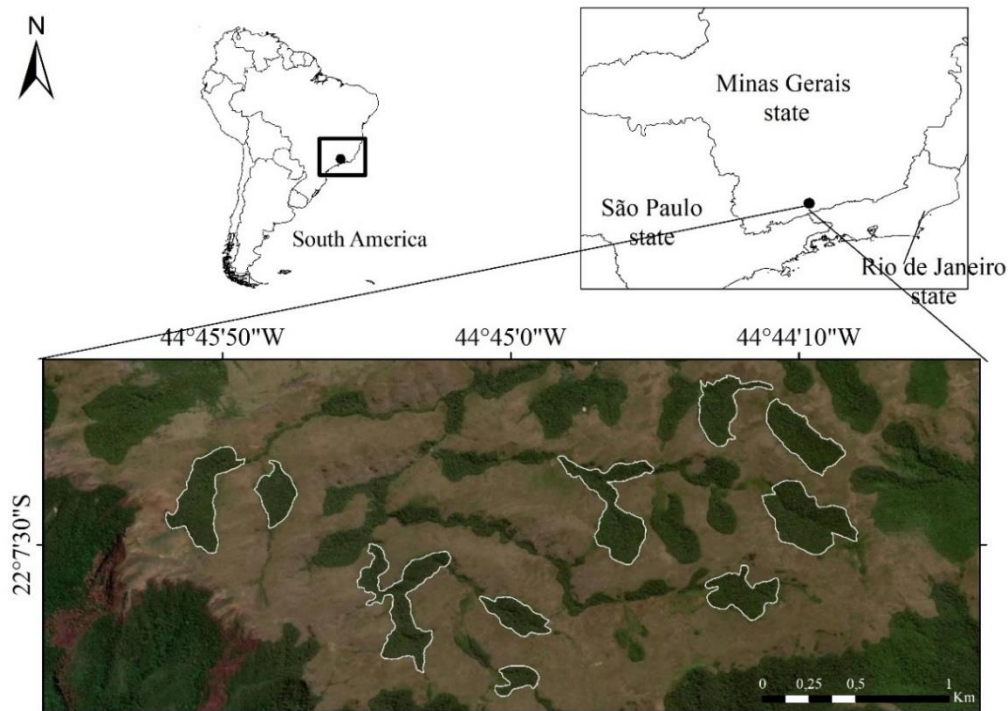
146

147 **2. Material and methods**

148 *Study areas*

149 Our study was carried out in the Serra do Papagaio State Park (PESP), a protected
150 area located in the Serra da Mantiqueira, Southeastern Brazil (22°7'34"S, 44°44'54"W)
151 (Fig. 1). The park is inserted in the Atlantic Forest domain and the portion where this
152 study was conducted is characterized by patches of Tropical Montane Cloud Forest
153 (TMCF) (*sensu* Fahey et al. 2016) surrounded by native non-forest vegetation (mostly
154 highland grasslands, rock outcrops and, in the least extent, wetlands) (Ribeiro et al., 2018;
155 Santana et al., 2021) (Fig. 2). Highland grasslands (*campos de altitude*) occur in lithosols
156 (shallow soils consisting of imperfectly weathered rock fragments), characterized by low
157 organic matter levels. In contrast, TMCF occurs in cambisols and histosols, that have at
158 least an incipient subsurface soil formation and high accumulation of organic matter and
159 moisture in the upper soil layers (IUSS Working Group WRB, 2015). The forest edges
160 with the grasslands were very sharp and the grasslands close to the edge were often
161 dominated by the shrubs *Baccharis platypoda* DC and *Croton alchorneicarpus* Croizat
162 (Santana et al., 2021) (Fig. 2).

163



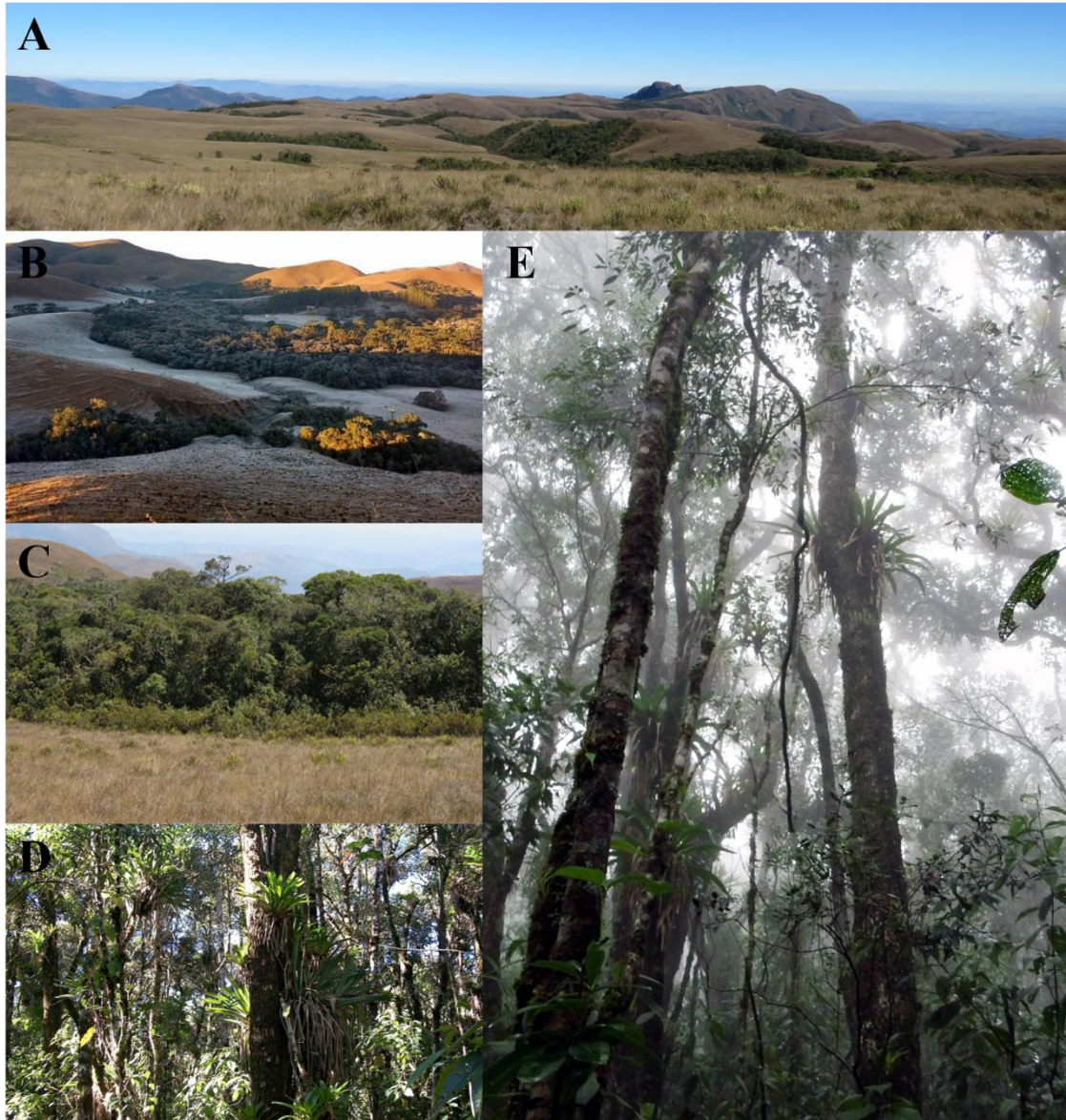
164

165 **Figure 1:** Location of the study area with delimitation of the 10 patches of tropical
 166 montane cloud forest (sampled in white), situated in southeastern Brazil. The brownish
 167 areas are the grasslands.

168

169 The studied forests patches ranged from 1800 to 2000 m of elevation. The region
 170 experiences a subtropical highland climate (Cwb type according to the Köppen climate
 171 classification), with rainy summers and cold and dry winters. The mean annual
 172 precipitation is 2060 mm, of which 80% is concentrated between October and March, but
 173 there is no fully dry month. In the driest months, the precipitation is around 30 and 90
 174 mm (Santana et al., 2021), but as the mist formation is constant over the year, some
 175 additional precipitation can result from the condensation of water droplets on the surface
 176 of plants (Bittencourt et al., 2019; Bruijnzeel et al., 2010, 2011). The mean annual
 177 temperature is 13.8° C. The minimum temperatures in the winter are usually between 0°

178 C and 10° C, with occasional frosts (Fig. 2B). The summer is mild, with the temperature
 179 in the hottest days usually lower than 30° C (Santana et al., 2021).



180

181 **Figure 2:** **A:** Tropical montane cloud forest patches surrounded by native grasslands. **B:**
 182 Detail of frost event (2016) occurred in the highland grasslands of study area. **C:** Natural
 183 edge with emphasis on sharp transition between the grassland and forest. **D:** Interior of
 184 cloud forest patch of the Serra do Papagaio State Park (PESP) with emphasis on the large
 185 amount of epiphytes. **E:** Forest interior, showing the crowds immersed in fog. Photos: A

186 and **D:** L.D. Santana; **B:** J.G.F. Mendonça and L. Mendes; **C:** E. van den Berg; **E:** J.H.C.
187 Ribeiro

188

189 *Vegetation sampling*

190 The tropical montane cloud forest patches (TMCF) were mapped using satellite
191 images and information gathered on field work. We selected 10 representative forest
192 patches ranging from 2 to 11 ha for sampling. In each forest, we established 10 permanent
193 sample plots (20 × 10 m), with five allocated right on the forest edge (longer side parallel
194 to the limit between the forest and the grassland), and five randomly distributed over the
195 forest interior (ranging from 20 m to 117 m from the limit with grassland, depending on
196 the forest size). Data from interior plots were provided by the authors of Ribeiro et al.
197 (2018) and edge plots by the authors of Santana et al. (2021). We sampled all trees in the
198 plots with a diameter at breast height (DBH, measured at 1.3 m above the ground) ≥ 5cm.
199 Our dataset covers a 2-ha sampling effort (1 ha for each forest habitat) and a total of 5495
200 trees distributed in 107 species.

201

202 *Functional Traits*

203 We collected functional traits for all species that reached five individuals or more
204 (edge and forest interior separately) in each habitat totaling a dataset with 5418 trees
205 distributed in 62 species. For these species, following Pérez-Harguindeguy et al. (2016),
206 we randomly selected five individuals and, for which one, we measured the traits: leaf
207 area (cm²), specific leaf area (mm²/mg⁻¹), leaf thickness (mm), petiole length (cm),
208 maximum diameter (cm), crown length ratio (m), crown area ratio (m) and wood density
209 (g /cm³) (see Table 1 with all functional traits and ecological significance).

210 **Table 1:** List with all functional traits collected, their ecological significance and expected pattern for each one in relation to the forest edge-interior
 211 transition. LA = leaf area; SLA = specific leaf area; LT = leaf thickness; PL = petiole length; D_{\max} = maximum diameter; CLR = crown length
 212 ratio; CAR = crown area ratio; WD = wood density.

Trait	Ecological significance	Expected Response	References
LA	Metric related to the ability of leaf to intercept light.	We expect individuals with larger LA in forest interior: larger leaves uptake a greater amount of light.	Lim et al. (2017); Pérez-Harguindeguy et al. (2013)
SLA	Trait closely related to the photosynthetic rate of plants and leaf longevity.	We expect individuals with lower SLA at the edges: lower SLA indicates reduction in the photosynthetic rate, however an increase in leaf longevity.	Bucher & Rosbakh (2021); Lim et al. (2017); Vergara-Gómez et al. (2019), Pérez-Harguindeguy et al. (2013)
LT	Plays a key role in determining the physical strength of leaves and is negatively linked to SLA.	We expect individuals with greater leaf thickness at the edges: plays a greater physical strength of leaves.	Borges et al. (2018); Pérez-Harguindeguy et al. (2013)
PL	Closely related to spatial positioning and hydraulic support of the leaf.	We expect individuals with larger LT in forest interior: larger petioles avoid overlapping leaves.	Pérez-Harguindeguy et al. (2013)
D_{\max}	Canopy support.	We expect individuals with higher D_{\max} in forest interior: larger diameters tend to occur in less stressful environments and with more resources.	Pérez-Harguindeguy et al. (2013); Silva et al. (2019)
CLR	Competitive strength of plant for light.	We expect higher CLR in the forest interior: individuals compete more for light.	Borges et al. (2018); Bucher & Rosbakh (2021); Pérez-Harguindeguy et al. (2013); Prado-Junior et al (2016)
CAR	Competitive strength of plant for light.	We expect lower CAR at the edge: habitat with higher wind intensity and individuals compete less for light.	Bucher & Rosbakh (2021); Pérez-Harguindeguy et al. (2013); Prado-Junior et al (2016)
WD	Component associated with hydraulic safety and resistance against physical damage.	We expect higher wood density at the edge: individuals with higher WD have more resistant woods.	Pérez-Harguindeguy et al. (2013); Prado-Junior et al (2016)

213

214 For the measurement of the leaf area (LA) and specific leaf area (SLA), we
215 collected five to ten fully expanded leaves without evidence of herbivory or pathogens
216 for each individual. To measure the leaf area (LA), we scanned the leaves with a metric
217 scale in a table scanner and, with the Image J software, we obtained the area.
218 Subsequently, we dried the leaves in an oven at 80° C for 48 hours and measured the
219 oven-dry mass (DM) in an analytical balance with an accuracy of 0.0001g. The specific
220 leaf area (SLA) was calculated using the ratio $LA \text{ (cm}^2\text{)} / DM \text{ (g)}$. Leaf thickness (LT)
221 and petiole length (PL) were obtained for the same leaves used to measure the leaf area.
222 With the aid of a digital caliper with an accuracy of 0.01 mm, we measured LT and, with
223 a measuring tape, we obtained PL for all the leaves before oven-dry them (Pérez-
224 Harguindeguy et al., 2013).

225 . For the same sampled individuals which we evaluated the leaf traits we also
226 measured the tree height (H, m), lower foliage height (LFH, m) and two perpendicular
227 projected crown diameters (the largest one and its correspondent perpendicular one). We
228 used the average of those diameters to calculate the crown area (CA) for each individual.
229 As allometric traits we calculated the crown area ratio (CAR - ratio between CA and H)
230 and the crown length ratio (CLR - ratio between $(H - LFH)$ and H) (Borges et al., 2018;
231 Prado-Junior et al., 2016). We obtained the maximum diameter (D_{\max}) of the species using
232 the 95th percentile of all the diameters of the individuals of the sampled species.

233 Finally, we obtained wood density (WD) using a segment (at least 7 cm in
234 circumference and 10 cm in length) of at least five individuals of each species removed
235 from a branch between second-fourth-order. After removing its bark, we submerged the
236 branch in water for three days. Following Chave (2006) and Falster and Westoby (2005),
237 we measured the volume of the samples using an analytical balance with an accuracy of
238 0.0001g, applying the water-displacement method. Subsequently, we dried the branches

239 in an oven at 70° C for 72 hours and measured their dry mass on an analytical balance.
240 The wood density was then calculated by the ratio between the dry mass and the volume
241 of water displaced.

242

243 *Community-Weighted Mean traits and Functional Diversity indices*

244 We used basal area of each plot as a weight factor to calculate the Community-
245 Weighted Mean (CWM) of the traits and diversity indices. We opted by the basal area as
246 the weight factor because it reflects better plant performance than number of individuals
247 (Prado-Junior et al., 2016).

248 For functional diversity (FD) indices we excluded traits that had a high
249 correlation. Thus, the FD was calculated using the following traits: CWM- Specific Leaf
250 Area (CWM_{SLA}), CWM-Petiole Length (CWM_{PL}), CWM-Maximum diameter
251 (CWM_{Dmax}), CWM- Crown Length Ratio (CWM_{CLR}), CWM-Wood Density (CWM_{WD})
252 (Appendix A). We assessed the FD using functional richness (FRic), functional
253 divergence (FDiv) and functional dispersion (FDis). FRic was used because it assesses
254 how much of the spectrum of a given resource (niche space) is being filled by the species
255 in a community. FDiv is related to how far the traits vary from the community traits'
256 average in a multivariate niche space – a high functional divergence indicates a high
257 degree of niche differentiation (Mason et al., 2005). And the FDis assesses the mean
258 distance of individual species traits to the centroid of all species in the community
259 (Laliberte & Legendre, 2010). The CWM and FD indices were calculated using the “FD”
260 package in R (Laliberté et al., 2014).

261

262 *Statistical analyses*

263 To evaluate interspecific trait variation and functional diversity (FRic, FDiv and
264 FDis) between habitats (edge and interior), we performed generalized linear mixed
265 models (GLMM) where traits values and FD indexes were the response variables and
266 habitat was a fixed factor as follow: $CWM\text{-}Traits \text{ and } FD = \text{Habitat} + (1 | \text{Patch})$. We
267 included the forest patch as a random effect to account for the nestedness of the plots
268 within each forest patch.

269 To evaluate the intraspecific functional trait variation for co-occurring species
270 between forest habitats (edge and interior) and how the habitats drive these variations, we
271 performed linear mixed models where habitat, species and the interaction between them
272 were fixed factors, and forest patches was a random factor as follow: $Traits = \text{Species} * \text{Habitat} + (1 | \text{Patch})$.

274 To evaluate the impact of using the intraspecific trait values (ITV) (i.e., species
275 trait values from their respective habitat – forest edge or interior) compared to excluding
276 intraspecific variation (i.e., mean value of species trait from both habitats) to compare the
277 community-weighted mean (CWM) trait values and the functional diversity indices
278 (functional richness, divergence and dispersion) between forest habitats, we set up two
279 scenarios. 1) *Including intraspecific variation* - this sampling scenario assumes that local
280 conditions play an important role in species trait variation, and hence, the sampling
281 strategy to compare functional metrics between communities must be focused in sampled
282 multiple individuals of each species across all sites. Thus, it is expected to find stronger
283 and more significant relationships between forest habitats when multiple values for each
284 species sampled in the contrasting habitats than using the mean values of species traits.
285 2) *Excluding intraspecific variation* – this sampling scenario assumes that intraspecific
286 trait variation is limited in importance, and hence, the sampling strategy to compare
287 functional metrics between communities would be to gather traits' data (e.g., including

288 global traits datasets) of as many species as possible. Thus, it is expected that results using
289 interspecific traits would be similar in significance and strength than those using
290 intraspecific traits. We compared the strength and significance of both scenarios by r^2
291 (adjustment of the models) and p-value ($p < 0.05$).

292 For those species that occurred in both habitats but were sampled only in one
293 habitat because in one of them they had less than 5 individuals, we used the value from
294 the other habitat, although their importance was very low, correspond to 0.24% and 0.42%
295 of total basal area of the edge and interior, respectively.

296 The analyzes were performed on the R software (R Development Core Team,
297 2017), using the following packages: FD (Laliberté et al., 2014), Vegan (Oksanen et al.,
298 2017), lme4 (Bates et al., 2014), lmerTest (Kuznetsova et al., 2016), MuMin (Barton,
299 2016) and car (Fox & Weisberg, 2019). For the graphical representations, the packages
300 used were: ggplot2 (Wickham & Chang, 2016), extrafont (Chang, 2016) and ggpubr
301 (Kassambara, 2020).

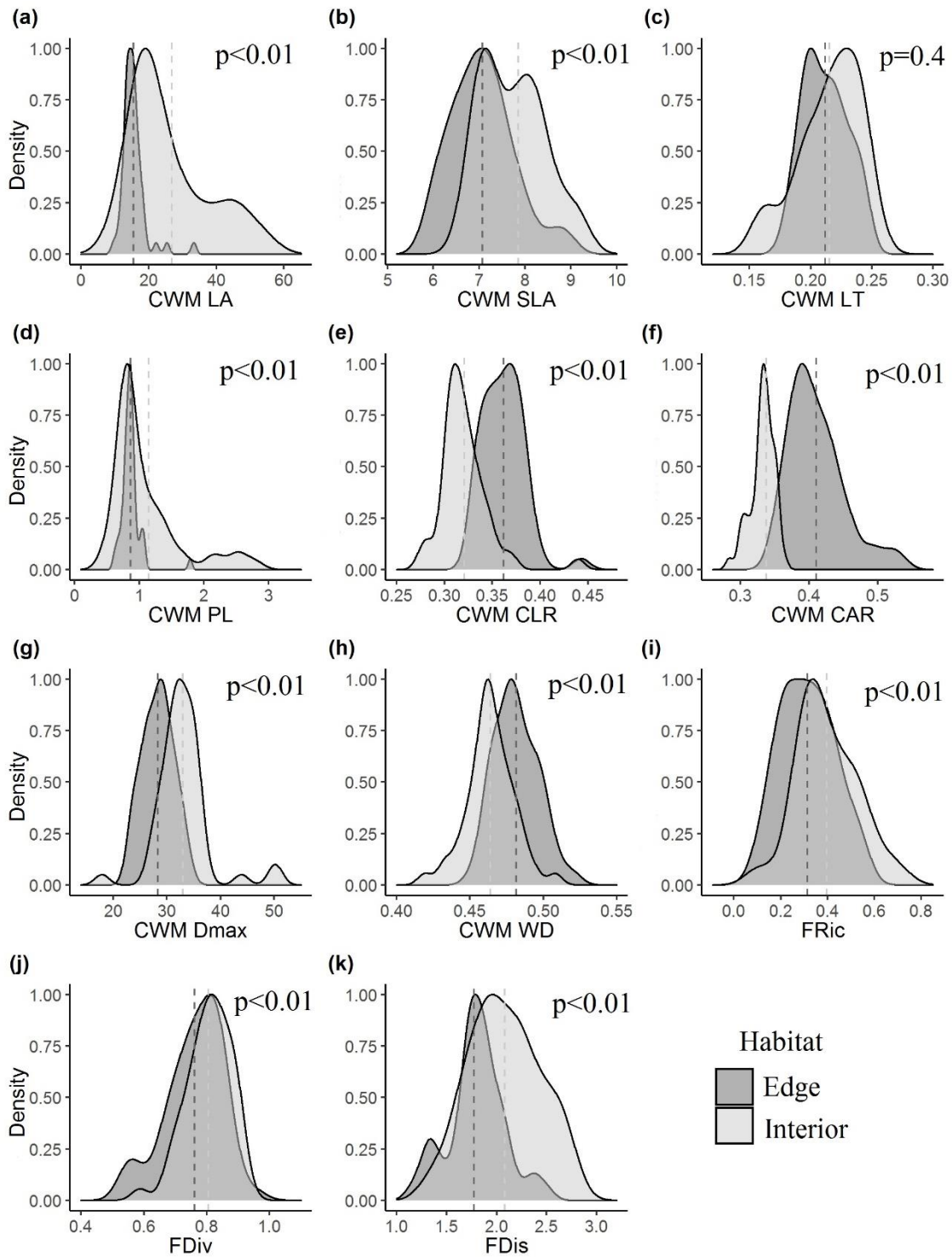
302

303 **3. Results**

304 We measured functional traits from 62 species, which 33 species were sampled in
305 both habitats, 17 species were exclusive from the forest edge and 12 species from the
306 forest interior (Appendix B). Regarding the functional diversity metrics, we found
307 CWM_{LA} , CWM_{SLA} , CWM_{PL} , CWM_{Dmax} , $FRic$, $FDiv$ and $FDis$ significantly higher in
308 forest interior than in edge when included intraspecific traits variation. CWM_{CLR} ,
309 CWM_{CAR} and CWM_{WD} were significantly higher in edge (Figure 3; Table 2). For all
310 CWM trait values and for all functional diversity indices, adjustment value of the models
311 (r^2) was higher when considering the intraspecific variation. In addition, to CWM_{SLA} ,

312 CWM_{CLR}, CWM_{CAR}, CWM_{WD}, FRic and FDiv differences between habitats were only
 313 detected ($p < 0.05$) when intraspecific variation was inserted (Table 2; Appendix C).

314



315

316 **Figure 3:** Comparison of functional traits and functional diversity (including intraspecific
317 variation) between edge and interior habitats of forest patches surrounded by natural
318 grasslands. CWM LA = community-weighted mean of leaf area; CWM SLA =
319 community-weighted mean of specific leaf area; CWM LT = community-weighted mean
320 of leaf thickness; CWM PL = community-weighted mean of petiole length, CWM CLR
321 = community-weighted mean of crown length ratio; CWM CAR = community-weighted
322 mean of crown area ratio; CWMDmax = community-weighted mean of maximum
323 diameter; CWM WD = community-weighted mean of wood density; FRic = functional
324 richness; FDiv = functional divergence; and FDis = functional dispersion. Dashed lines
325 represent the average values of each variable per habitat.

326

327 **Table 2:** Comparison of functional metrics between edge and interior habitats through the inclusion and exclusion of intraspecific variation.
 328 Abbreviation: s.e. = standard deviation; Coef = Standardized multiple regression coefficient; r^2 = adjustment value of the models. * = p-value <
 329 0.05. Acronyms of functional metrics according to Figure 3.

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Traits/ FD indices	Functional metrics' values by habitat including intraspecific variation					Functional metrics' values by habitat excluding intraspecific variation				
	Mean \pm s.e. Edge	Mean \pm s.e. Interior	Coef.	r^2	p-value	Mean \pm s.e. Edge	Mean \pm s.e. Interior	Coef.	r^2	P-value
CWM.LA (cm ²)	15.49 \pm 0.69	26.82 \pm 13.26	0.203	0.32	<0.01*	17.17 \pm 3.86	24.79 \pm 12.79	0.120	0.13	<0.01*
CWM.SLA (mm ² /mg ⁻¹)	7.07 \pm 0.69	7.86 \pm 0.90	0.045	0.21	<0.01*	7.36 \pm 0.69	7.43 \pm 0.87	0.003	0.00	0.7
CWM.LT (mm)	0.21 \pm 0.02	0.22 \pm 0.03	0.003	0.01	0.4	0.21 \pm 0.02	0.21 \pm 0.02	0.000	0.00	0.9
CWM.PL (cm)	0.87 \pm 0.16	1.14 \pm 0.66	0.046	0.08	<0.01*	0.87 \pm 0.19	1.12 \pm 0.62	0.043	0.07	<0.01*
CWM.CLR (m)	0.36 \pm 0.02	0.32 \pm 0.03	-0.035	0.44	<0.01*	0.34 \pm 0.01	0.34 \pm 0.02	-0.004	0.01	0.3
CWM.CAR (m)	0.41 \pm 0.04	0.34 \pm 0.04	-0.086	0.51	<0.01*	0.37 \pm 0.02	0.37 \pm 0.04	0.000	0.00	0.9
CWM.D _{max} (cm)	28.30 \pm 2.86	32.98 \pm 5.07	0.064	0.26	<0.01*	28.30 \pm 2.86	33.16 \pm 5.05	0.066	0.26	<0.01*
CWM.WD (g/cm ³)	0.48 \pm 0.01	0.46 \pm 0.02	-0.018	0.25	<0.01*	0.47 \pm 0.01	0.47 \pm 0.02	-0.003	0.01	0.3
FRic	0.31 \pm 0.12	0.4 \pm 0.13	0.071	0.10	<0.01*	0.26 \pm 0.10	0.30 \pm 0.11	0.033	0.03	0.07
FDiv	0.76 \pm 0.09	0.81 \pm 0.07	0.026	0.07	<0.01*	0.77 \pm 0.09	0.80 \pm 0.08	0.018	0.03	0.08
FDis	1.77 \pm 0.32	2.08 \pm 0.35	0.110	0.16	<0.01*	1.77 \pm 0.30	2.01 \pm 0.36	0.088	0.11	<0.01*

340 When we evaluate the intraspecific functional trait variation for co-occurring species
 341 between forest habitats (edge and interior), we found a significant interaction for CLR, CAR,
 342 PL, LA and SLA (Table 3). WD showed significant difference between habitats, but did not
 343 show habitat \times species interaction. Species had a significant effect on all traits (Table 3).

344

345 **Table 3:** Results of model analyses used to evaluate influence of habitat on the functional
 346 traits of co-occurring species in the edge and interior of forest patches. * = p-value < 0.05.

347 Acronyms of functional traits: LA = leaf area; SLA = specific leaf area; LT = leaf thickness;

348 PL = petiole length, CLR = crown length ratio; CAR = crown area ratio; WD = wood density

Traits	Habitat		Species		Habitat x Species	
	F	p-value	F	p-value	F	p-value
LA	2.24	0.13	45.65	<0.01*	4.12	<0.01*
SLA	0.93	0.33	7.95	<0.01*	1.59	0.02 *
LT	152	0.21	2.88	<0.01*	1.08	0.35
PL	0.01	0.91	47.44	<0.01*	3.38	<0.01*
CLR	5.50	<0.01*	2.06	<0.01*	1.51	0.04 *
CAR	0.12	0.72	4.52	<0.01*	1.4	0.06 *
WD	5.59	<0.01*	16.22	<0.01*	1.32	0.12

349

350 4. Discussion

351 We showed for the studied forest patches that edges surrounded by native grassland and
 352 forest interior are contrasting habitats in terms of functional traits and functional diversity. As
 353 we expected, the functional traits variation responded strongly to the inherent environmental
 354 differences between the habitats. Edge habitats showed individuals with functional traits that
 355 alleviate the stress caused by the environmental conditions of this habitat, such as reducing SLA
 356 and increasing wood density (WD). In contrast, forest interior showed individuals with trait
 357 values that intensify sunlight capture, such as larger leaves and petioles. The edge also proved

358 to be a more selective habitat in terms of range of functional traits, that is, it has strong
359 environmental filters, which reflected in the lower functional diversity.

360 In addition, we showed that intraspecific variation (ITV) plays an important role to the
361 establishing of individuals in contrasting habitats, in other words, the relationship between
362 functional traits and habitats were higher when the ITV was included. The phenotypic variation
363 of the functional traits is driven by the environmental differences of habitats. Therefore,
364 ignoring ITV in ecological studies that approach functioning mechanisms of communities can
365 result in wrong interpretations, especially when leaf and trunk data of plants are used.

366

367 *Spatial differentiation in functional traits and functional diversity indices*

368 As we expected, we found a strong variation in plant functional traits between edge and
369 interior habitats. Edges compared to forest interior are more subject to external pressures
370 (Appendix D) (e.g. lower air and soil moisture, higher and more variable temperatures, fire and
371 frost events, strong winds and greater light incidence) (Magnago et al., 2015; van den Berg &
372 Santos, 2003) and the individuals that occupy such habitat must have morphological and
373 physiological adaptations, measured here by functional traits, that allow them to deal with those
374 conditions (Silva et al., 2019). Lower LA and SLA reduce excessive transpiration of leaves and
375 minimize the water deficit in edges (Hoffmann & Franco, 2003; Wright et al., 2017, 2004). In
376 contrast, in interior habitat light is a limiting factor and individuals with larger leaves can
377 intercept a greater amount of light (Prado-Junior et al., 2016). In addition, larger petioles, as we
378 found for the interior, decrease the self-shading and minimize leaf overlap along the branch,
379 allowing better use of the light beam (Gianoli, 2001; Niinemets, 2010).

380 Although we expected smaller CLR and CAR at the edges due to the greater intensity
381 of the winds, the interior habitat that showed shallower tree crowns. Trees in forest interior
382 competes more for vertical light and crown area expansion through increased branch production

383 and horizontal extension would be restricted by competition with neighboring trees (Alves &
384 Santos, 2002). Under these conditions growth in height is favored reducing both CAR and CLR
385 ratios (Borges et al., 2018). In addition, besides the light intercepted by the top of the canopy,
386 individuals on the edge also receive lateral light, thus investing in the crown area and length in
387 these conditions (both resulting in reduction of CLR and CAR) can be advantageous (Silva et
388 al., 2019). Furthermore, a higher investment in crowns increase total surface to capture
389 humidity from fog, which might act as a solution for the drier soils in the edge (Borges et al.,
390 2018).

391 We predicted that the trees would have lower D_{\max} at the edges, because of smaller trees
392 are less likely to be uprooted by wind gusts (Laurance & Curran, 2008; Walker, 1991). Lower
393 D_{\max} also reflects the soil resource limitations (e.g. phosphorus content) and water deficit at the
394 edges that can restrict tree growth (Hoffmann et al., 2012; Silva et al., 2019). As we expected,
395 we found high WD at the edges, another functional trait that gives greater mechanical strength
396 to trees, in addition to providing greater hydraulic safety (Díaz et al., 2016; Pérez-Harguindeguy
397 et al., 2013).

398 Forest patches in montane ecosystems, as in the present study, are frequently affected
399 by frosts (Aparecido et al., 2018; Spehn et al., 2010) and these events may also have contributed
400 to spatial pattern of functional traits found, although most of the times they are neglected
401 (Bucher & Rosbakh, 2021; Lim et al., 2017). In woody communities, tree canopies modify
402 surface energy balances and thereby cause a local warming effect, in which temperatures are
403 higher under the trees crown (D'Odorico et al., 2013; Devaney et al., 2017; Hoffmann et al.,
404 2019). Forest cover can improve temperatures during frost events by as much as 5°C (Hoffmann
405 et al., 2019). However, in adjacent areas (grasslands) where the tree cover is low, temperatures
406 reach easily a few degrees below freezing in the area, forming a layer of cold air that collides
407 with the forest edge (Devaney et al., 2017; Hoffmann et al., 2019). And exposure to low

408 temperatures can alter plant development and cause significant damage in vegetative and
409 reproductive structures and even promote trees death (Bucher & Rosbakh, 2021; D’Odorico et
410 al., 2013). Therefore, the occurrence of frosts is a stronger filter on the edges, selecting those
411 individuals who present traits allowing their survival in such conditions. In this sense, there is
412 a direct relationship between greater resistance to frosts and conservative resource-use strategy
413 (Bucher & Rosbakh, 2021; Lim et al., 2017), because according to plant economic spectrum,
414 slow-growing individuals invest in production of leaves and stems more resistant to
415 environmental stress and with longer life (Díaz et al., 2016; Verbeeck et al., 2019; Wright et
416 al., 2004). Therefore, high WD and low SLA in the edges, for example, confirm this trade-off
417 and indicates that species are adopting a stress tolerant strategy there.

418 As we hypothesized, we found all metrics of functional diversity (FRic, FDiv, FDis)
419 higher in the forest interior. Again, this pattern agrees with the more stressful habitat presented
420 by the edges, where microclimatic conditions are more variable, water deficit is higher and
421 frosts are stronger (Dreyer et al., 2020; Silva et al., 2019; van den Berg & Santos, 2003).
422 Therefore, the species that survive in these locals are possibly converging in terms of stress
423 tolerant traits, limiting the range of each trait and reducing functional diversity (Botta-Dukát &
424 Czúcz, 2016; Götzenberger et al., 2012). In addition, a high number of species with similar
425 functions indicates greater functional redundancy (Magnago et al., 2014; Walker, 1992),
426 reducing the impact of species loss in the ecosystem functioning. This can be particularly
427 important on the edges, where mortality (and recruitment) is high and the community is very
428 dynamic (Bragion et al., 2018; Nunes et al., 2018). Therefore, summarizing, the functional
429 redundancy increase the resilience of the edges to their more unpredictable environmental
430 conditions (Laliberté et al., 2010).

431

432 *The role of intraspecific variation in functional ecology*

433 As we expected, we showed a strongly influence of habitats on intraspecific trait
434 variation (ITV) values. Even on small spatial scales, the environmental variation can be large,
435 such as differences in light incidence, edaphic conditions and wind intensity (Bragion et al.,
436 2018; Coelho et al., 2018; Magnago et al., 2015; Niinemets, 2010). In such conditions high
437 variation in functional traits can increase the species success since they can respond easily to
438 the micro-variation of local conditions (Borges et al., 2018; Silva et al., 2019; Vergara-Gómez
439 et al., 2019). High intraspecific variability can allow the species work as “jack of all trades”
440 organisms in heterogeneous or transitional habitats, such as forest edges, increasing the species
441 success there (Fréjaville et al., 2019; Pérez-Ramos et al., 2019; Umaña & Swenson, 2019).

442 In addition, as expected, the statistically significant differences between habitats in
443 relation to traits and functional diversity were best observed with the inclusion of intraspecific
444 variation, where it allowed the detection of effects in 11 variables, whereas the non-inclusion
445 of variation detected differences only in four of variables. And in all cases, the greatest
446 adjustment of the models (r^2) was verified when the ITV was included, indicating higher
447 explanatory capability. Despite the widely recognized importance of the ITV, most indices of
448 functional diversity (FD) working with multiple traits neglected it, using average trait values
449 for species (Albert et al., 2010, 2012; Cianciaruso et al., 2009). However, even two
450 communities with the same species composition and abundance could potentially have different
451 trait distributions and thus different FD because of the ITV (Albert et al., 2012). In the present
452 study we showed that disregarding the ITV may end up generating completely misleading
453 results, supporting the need of collecting data of multiple individuals of the same species for
454 correct assess of the FD. Furthermore, inclusion of ITV should improve our understanding of
455 how environmental changes affect the patterns of community functional diversity, mainly on
456 small spatial scales (Chalmandrier et al., 2017; Jung et al., 2010).

457 In a global review on intraspecific trait variation, seeking to understand which traits may
458 be more variable, Siefert et al. (2015) recommend that studies associated with leaf economic
459 traits, including the SLA, should include the intraspecific variation as they are responsible for
460 a significant proportion the total variation of characteristics within and among the community.
461 Besides the traits associated with the leaves, we strongly recommend the same procedure for
462 allometric traits (CLR, CAR) and wood density (WD), since we found these traits the most
463 affect ones by the inclusion of the intraspecific variation. For these traits the adjustment of the
464 models (r^2) went from 0 or 0.01 to values ranging between 0.25 and 0.51.

465

466 **5. Conclusions**

467 Our study showed that edge effect in natural forest patches is capable of altering traits
468 and functional diversity when compared to the interior habitat. Some studies had already
469 demonstrated these differences, however, all of them were done in man-made forest fragments
470 (Dreyer et al., 2020; Magnago et al., 2014), which highlights the importance of the present
471 study. Due to similarities in functioning, natural forest edges might serve as a reference for
472 future states of edges originated from anthropogenic fragmentation process. To support those
473 decisions, other studies that include forest patches with natural edges in different environmental
474 conditions and that incorporate forest dynamics are necessary.

475 In addition, we showed that intraspecific variation plays an important role in
476 establishing species in contrasting habitats. Neglecting this variation in functional diversity
477 studies, especially those that incorporate quantitative variables, can result in misinterpretations
478 about ecological patterns. Considering our results, we advise to extreme caution in relation to
479 the use of taxonomical levels above species to calculate trait values in absence of data or the
480 use of average trait values of distinct habitats. In both cases, a large parcel of trait variation
481 would be obliterated reducing considerably the chances of detecting real relationships between

482 environment and traits. Such strategies only should be used in large-scale studies, when the
 483 inclusion of intraspecific traits variation loses importance in relation to the variation linked to
 484 interspecific differences (Chalmandrier et al., 2017; Siefert et al., 2015).

485

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496

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498

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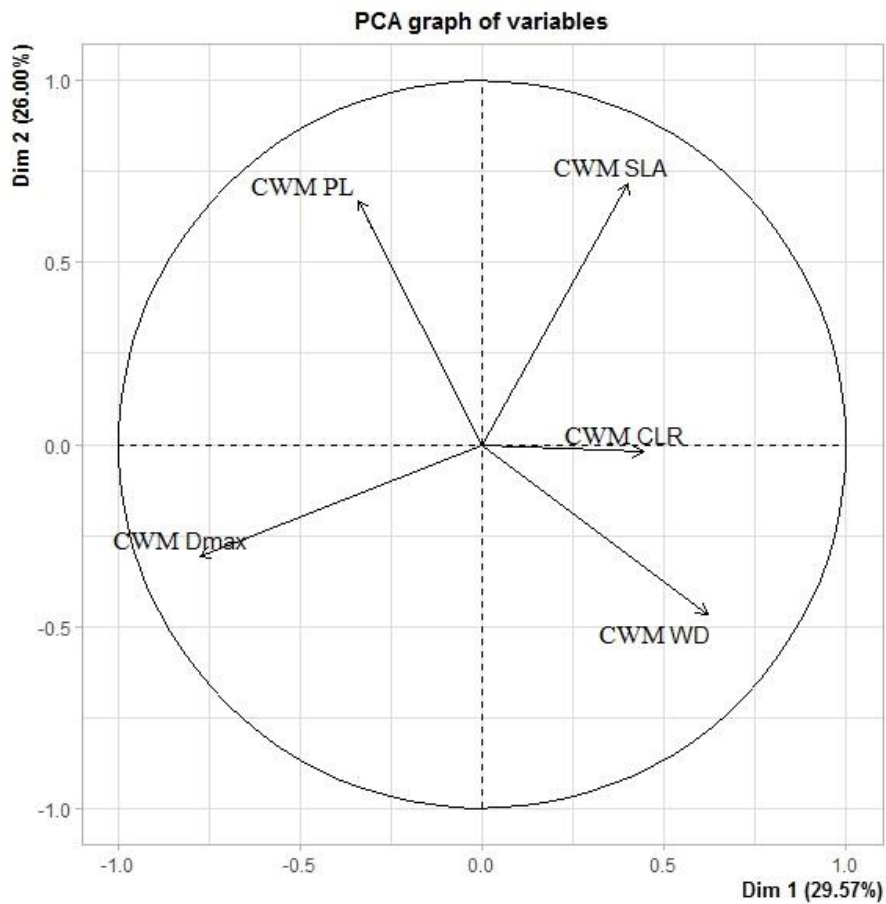
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805 **Supplementary material**

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807 **Appendix A:** Principal Component Analysis (PCA) diagram showing functional traits used to

808 calculate functional diversity.



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816 **Appendix B:** List of species studied with respective occurrence at edges or interior habitat of
 817 cloud forest patches surrounded by natural grasslands.

Species	Family	Occurrence	
		Edge	Interior
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	Euphorbiaceae	X	X
<i>Byrsonima ligustrifolia</i> A.Juss.	Malpighiaceae	X	X
<i>Cabralea canjerana</i> (Vell.) Mart.	Meliaceae	X	X
<i>Clethra scabra</i> Pers.	Clethraceae	X	X
<i>Cordia concolor</i> (Cham.) Kuntze	Rubiaceae	X	X
<i>Croton alchorneicarpus</i> Croizat	Euphorbiaceae	X	X
<i>Drimys brasiliensis</i> Miers	Winteraceae	X	X
<i>Ilex microdonta</i> Reissek	Aquifoliaceae	X	X
<i>Macropelus dentatus</i> (Perkins) I.Santos & Peixoto	Monimiaceae	X	X
<i>Miconia budlejoides</i> Triana	Melastomataceae	X	X
<i>Miconia pusilliflora</i> (DC.) Naudin	Melastomataceae	X	X
<i>Monteverdia gonoclada</i> (Mart.) Biral	Celastraceae	X	X
<i>Myrceugenia bracteosa</i> (DC.) D.Legrand & Kausel	Myrtaceae	X	X
<i>Myrceugenia regnelliana</i> (O.Berg) D.Legrand & Kausel	Myrtaceae	X	X
<i>Myrcia laruotteana</i> Cambess.	Myrtaceae	X	X
<i>Myrcia retorta</i> Cambess.	Myrtaceae	X	X
<i>Myrcia splendens</i> (Sw.) DC.	Myrtaceae	X	X
<i>Myrcia subcordata</i> DC.	Myrtaceae	X	X
<i>Myrcia venulosa</i> DC.	Myrtaceae	X	X
<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	Myrtaceae	X	X
<i>Myrsine gardneriana</i> A.DC.	Primulaceae	X	X
<i>Myrsine umbellata</i> Mart.	Primulaceae	X	X
<i>Ocotea corymbosa</i> (Meisn.) Mez	Lauraceae	X	X
<i>Ocotea pulchella</i> (Nees & Mart.) Mez	Lauraceae	X	X
<i>Pimenta pseudocaryophyllus</i> (Gomes) Landrum	Myrtaceae	X	X
<i>Prunus myrtifolia</i> (L.) Urb.	Rosaceae	X	X
<i>Psychotria vellosiana</i> Benth.	Rubiaceae	X	X
<i>Roupala montana</i> Aubl.	Proteaceae	X	X
<i>Schefflera calva</i> (Cham.) Frodin & Fiaschi	Araliaceae	X	X
<i>Siphoneugena crassifolia</i> (DC.) Proenãsa & Sobral	Myrtaceae	X	X
<i>Symplocos insignis</i> Brand	Symplocaceae	X	X
<i>Symplocos revoluta</i> Casar.	Symplocaceae	X	X
<i>Vernonanthura discolor</i> (Spreng.) H.Rob.	Asteraceae	X	X
<i>Baccharis oreophila</i> Malme	Asteraceae	X	
<i>Eremanthus erythropappus</i> (DC.) MacLeish	Asteraceae	X	
<i>Frangula sphaerosperma</i> (Sw.) Kartesz & Gandhi	Rhamnaceae	X	
<i>Huberia nettoana</i> Brade	Melastomataceae	X	
<i>Ilex</i> sp.	Aquifoliaceae	X	
<i>Ilex theezans</i> Mart. ex Reissek	Aquifoliaceae	X	
<i>Leandra aurea</i> (Cham.) Cogn.	Melastomataceae	X	

<i>Myrceugenia miersiana</i> (Gardner) D.Legrand & Kausel	Myrtaceae	X
<i>Myrcia guianensis</i> (Aubl.) DC.	Myrtaceae	X
<i>Myrcia montana</i> Cambess.	Myrtaceae	X
<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	Primulaceae	X
<i>Myrsine lancifolia</i> Mart.	Primulaceae	X
<i>Ouratea semiserrata</i> (Mart. & Nees) Engl.	Ochnaceae	X
<i>Piptocarpha axillaris</i> (Less.) Baker	Asteraceae	X
<i>Piptocarpha regnellii</i> (Sch.Bip.) Cabrera	Asteraceae	X
<i>Podocarpus lambertii</i> Klotzsch ex Endl.	Podocarpaceae	X
<i>Symplocos falcata</i> Brand	Symplocaceae	X
<i>Araucaria angustifolia</i> (Bertol.) Kuntze	Araucariaceae	X
<i>Eugenia widgrenii</i> Sond. ex O.Berg	Myrtaceae	X
Indeterminate	Indeterminate	X
<i>Jacaranda cuspidifolia</i> Mart.	Bignoniaceae	X
<i>Leandra carassana</i> (DC.) Cogn.	Melastomataceae	X
<i>Miconia</i> sp.	Melastomataceae	X
<i>Miconia latecrenata</i> (DC.) Naudin	Melastomataceae	X
<i>Miconia sellowiana</i> Naudin	Melastomataceae	X
<i>Mollinedia</i> sp.	Monimiaceae	X
<i>Myrceugenia rufescens</i> (DC.) D.Legrand & Kausel	Myrtaceae	X
<i>Nectandra grandiflora</i> Nees	Lauraceae	X
<i>Ocotea odorifera</i> (Vell.) Rohwer	Lauraceae	X

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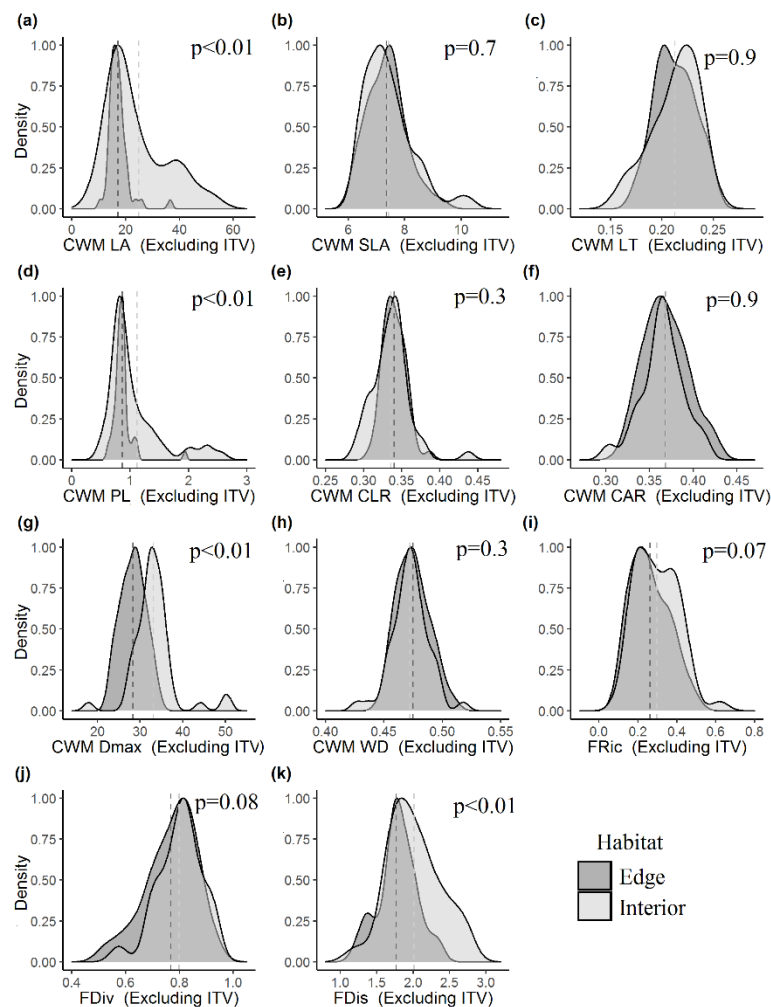
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828 **Appendix C:** Comparison of functional traits and functional diversity (excluding intraspecific
 829 trait variation (ITV)) between edge and interior habitats of forest patches surrounded by natural
 830 grasslands. CWM LA = community-weighted mean of leaf area; CWM SLA = community-
 831 weighted mean of specific leaf area; CWM LT = community-weighted mean of leaf thickness;
 832 CWM PL = community-weighted mean of petiole length, CWM CLR = community-weighted
 833 mean of crown length ratio; CWM CAR = community-weighted mean of crown area ratio;
 834 CWMDmax = community-weighted mean of maximum diameter; CWM WD = community-
 835 weighted mean of wood density; FRic = functional richness; FDiv = functional divergence;
 836 and FDis = functional dispersion. Dashed lines represent the average values of each variable
 837 per habitat.



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839 **Appendix D:** Comparative table of environmental resources/ conditions found in edge and
 840 interior habitats of forest patches.

Resources/conditions	Edge	Interior	Information source
Phosphorus content	Lower	Higher	Santana et al. (2021)
Soil moisture	Lower	Higher	van den Berg & Santos (2003)
Clay %	Higher	Lower	Santana et al. (2021)
Organic matter	Lower	Higher	Santana et al. (2021)
Light	Higher	Lower	van den Berg & Santos (2003)
Wind incidence	Higher	Lower	Magnago et al., 2015
Frost intensity	Higher	Lower	Dreyer et al. (2020)
Fire frequency	Higher	Lower	Silva et al. (2019)

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