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Diversidade de anfíbios anuros ao longo de gradientes elevacionais na Mata Atlântica: padrões e processos

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padrões e processos

O presente trabalho em nível de Doutorado foi avaliado e aprovado, em 8 de junho de 2022, pela banca examinadora composta pelos seguintes membros:

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RESUMO

Desde o início do Século XIX até os dias atuais, a busca por entender como a biodiversidade está organizada de forma espacial e temporal tem sido um dos principais desafios na ecologia e na biogeografia. Por exemplo, apesar de sabermos que a diversidade varia ao longo dos gradientes elevacionais, os mecanismos subjacentes aos padrões de distribuição das espécies ainda são pouco conhecidos, principalmente ao longo das regiões tropicais e subtropicais. No presente trabalho utilizei então os anfíbios anuros como organismos modelo para tentar entender como se dão os processos de estruturação e formação das assembleias encontradas ao longo de um gradiente elevacional localizado na porção subtropical da Mata Atlântica brasileira. No primeiro capítulo, busquei investigar o padrão geral da distribuição da diversidade, bem como a variação na composição das assembleias de anuros ao longo desse gradiente. Adicionalmente, avaliei como que as características espaciais e ambientais estão relacionadas com os padrões observados. No segundo capítulo, investiguei como a sazonalidade climática típica da região subtropical poderia estar relacionada com os padrões de diversidade observados, tentando entender especificamente o papel da variação da temperatura nesse sistema. Os resultados aqui apresentados revelam que os padrões de distribuição de anuros ao longo de gradientes elevacionais da Mata Atlântica estão relacionados com a variação da temperatura, bem como com a quantidade de remanescentes de habitats naturais. Também que a sazonalidade exerce um papel importante na estruturação das assembleias ao longo do gradiente elevacional, reforçando a influência das adaptações fisiológicas das espécies de anuros na determinação dos padrões de diversidade observados. Tendo em vista que a variação da temperatura média se mostrou um fator chave na estruturação das assembleias de anuros, esses resultados podem ser utilizados no desenvolvimento de estratégias de conservação mais efetivas frente às mudanças climáticas globais. Assim, esse estudo contribui para o melhor entendimento dos padrões de distribuição da biodiversidade, e reforça a importância dos ambientes montanos para a manutenção da mesma.

Palavras-chave: Anfíbios, gradiente altitudinal, Mata Atlântica, Neotrópicos, sazonalidade.

ABSTRACT

From the beginning of the 19th century to the present day, understanding how biodiversity is organized spatially and temporally remains one of the main challenges in ecology and biogeography. For example, although we know that diversity changes along elevational gradients, the mechanisms underlying species distribution patterns are still poorly understood, especially across tropical and subtropical regions. Here, I used anuran amphibians as model organisms to try to understand how the community is structured and how assembly processes work along an extensive elevational gradient in the subtropical portion of the Brazilian Atlantic Forest. In the first chapter we sought to investigate the general diversity patterns as well as the variation in the composition of anuran assemblages along the gradient. Additionally, we evaluated how the spatial and environmental characteristics are related to the observed patterns. In the second chapter we investigate how the typical climatic seasonality of the subtropical region could be related to these patterns, trying to understand specifically the role of temperature variation in this system. The results presented here suggest that the patterns of frog diversity along elevation gradients in the Atlantic Forest are related to variation in temperature, and that more extensive natural habitat areas retain more diversity. Additionally, seasonality plays an important role in the structuring frog assemblages along the elevation gradient, reinforcing the influence of species physiological adaptations in determining the observed diversity patterns. Given that the variation of mean temperature proved to be a key factor structuring anuran assemblages, these results can be used in the development of more effective conservation strategies in the face of global climate change. Thus, this study contributes to a better understanding of biodiversity distribution patterns, and reinforces the importance of mountain for its maintenance.

Keywords: Amphibians, Atlantic Forest, elevational gradient, Neotropics, seasonality.

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1 INTRODUÇÃO GERAL

1.1 PADÕES DE DISTRIBUIÇÃO DA BIODIVERSIDADE

A diversidade das mais diferentes formas de vida não se distribui de forma homogênea por toda a superfície do planeta. Tal discrepância é facilmente notada ao compararmos, por exemplo, as florestas tropicais úmidas com os desertos áridos; ou as florestas de encostas com os campos nos topos das montanhas. Entender como essa biodiversidade varia ao longo dos mais diversos tipos de gradientes ambientes tem sido tema central de estudos ecológicos e biogeográficos nos últimos dois séculos (Gaston, 2000; Lomolino, 2001). Dentre os padrões de distribuição, o mais reconhecido, e talvez o mais estudado, seja o de declínio do número de espécies da região equatorial em direção aos polos (Figura 1; Pianka, 1966; Rohde, 1992; Willig et al., 2003). Denominado de gradiente latitudinal de diversidade, estudos desenvolvidos com os mais diversos grupos taxonômicos indicam determinada consistência e robustez desse padrão (Barthlott et al., 2007; Fuhrman et al., 2008; Harriott & Banks, 2002; Willig et al., 2003), embora existam algumas exceções (Price et al., 1998).

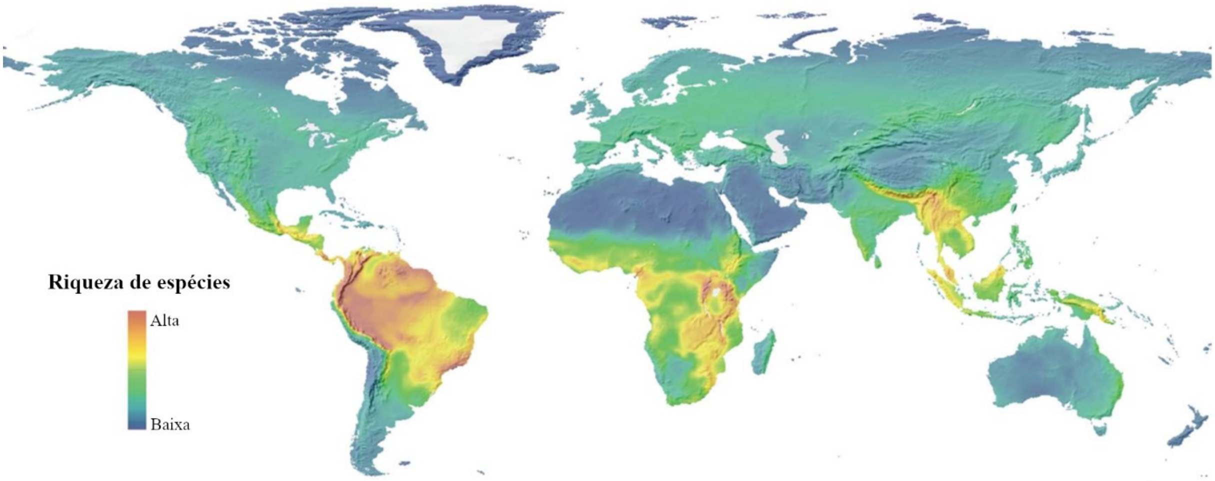

Figura 1. Padrão global de riqueza de espécies de vertebrados (anfíbios, aves e mamíferos), superposta em mapa topográfico. Adaptado de Rahbeck et al. (2019).

Desde o século XIX, importantes naturalistas como Alfred Russel Wallace, Alexander von Humboldt e Charles Darwin já tinham reconhecido e descrito o gradiente latitudinal de diversidade (Lomolino, 2001). E ao longo de expedições realizadas em regiões tropicais, estes mesmos naturalistas identificaram um outro tipo de padrão de distribuição da diversidade. As observações feitas por von Humboldt (1849) ao longo do Monte Chimbozaro nos Andes equatorianos, por Darwin (1859) nos Andes chilenos, e Wallace (1878) na Indonésia, levaramlos a concluir que, ao longo de um gradiente elevacional, a diversidade tende a diminuir das partes baixas para as mais elevadas. Esse padrão, que faz um paralelo com o gradiente latitudinal por muito tempo foi considerado a resposta geral para todos os organismos (Lomolino, 2001; Terborgh, 1977, 1985). Entretanto, o desenvolvimento de estudos empíricos com múltiplos grupos taxonômicos em montanhas espalhadas por todo o globo (e.g. Grinnell et al., 1930; Longino & Branstetter, 2019; Whittaker, 1960; Zu et al., 2019), em conjunto com trabalhos de revisão sobre o tema (e.g. Beck et al., 2017; McCain, 2005, 2010; McCain & Beck, 2016; Rahbek, 1995, 2005), apontam uma maior diversidade de respostas. Dessa forma, hoje são reconhecidos quatro padrões principais de distribuição da diversidade ao longo de gradientes elevacionais (Figura 2; McCain, 2009).

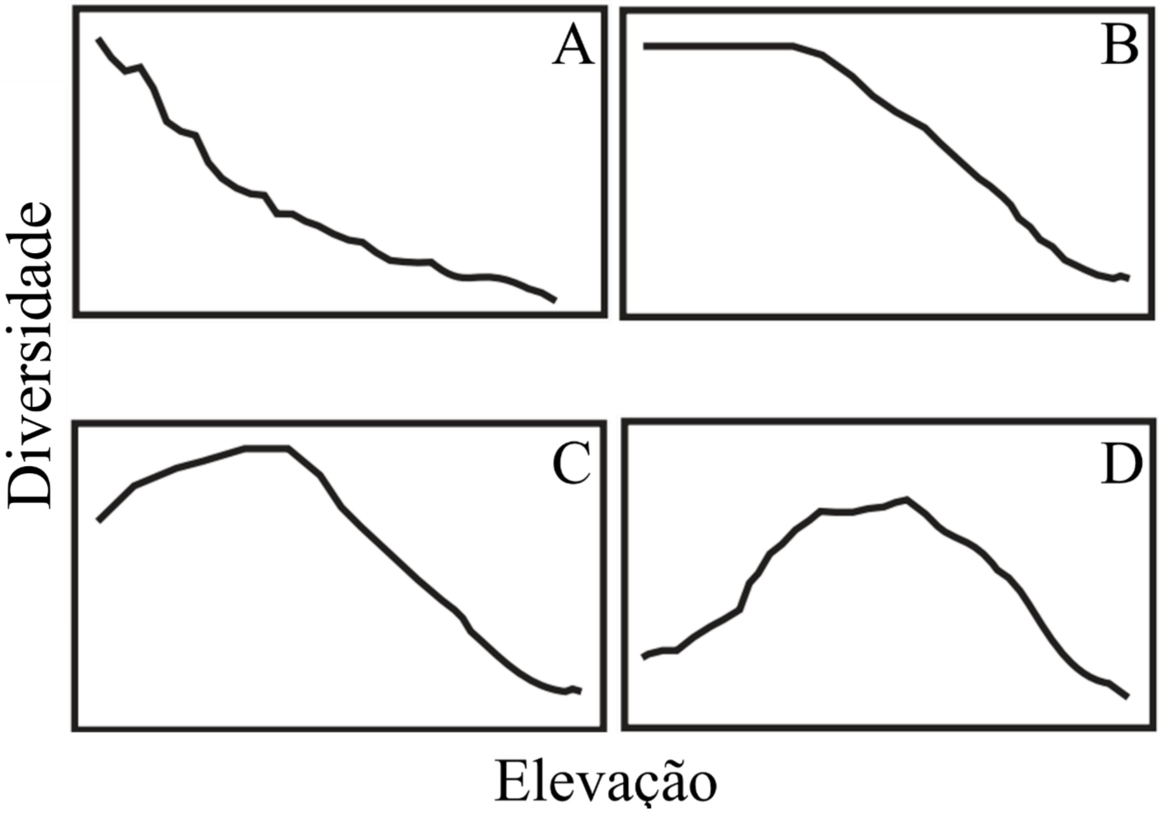

Figura 2. Quatro principais padrões de distribuição de diversidade ao longo de gradientes elevacionais. A: Decréscimo linear; B: Baixo platô; C: Baixo platô com pico intermediário; D: Pico em elevações intermediárias. Adaptado de McCain & Grytnes (2010).

O primeiro destes padrões corresponde ao primeiro previamente relatado, que seria correspondente ao de declínio contínuo da diversidade com o aumento da elevação (Figura 2A). Um segundo possível padrão é de baixo platô, onde valores elevados de diversidade são encontrados consecutivamente ao longo de baixas elevações, seguido então de um decréscimo ao longo de médias e altas elevações (Figura 2B). Um terceiro padrão considerado é o de baixo platô com pico em elevações intermediárias, no qual valores elevados de diversidade são encontrados continuamente ao longo das baixas elevações, seguido de um pico em elevações intermediárias, com subsequente decréscimo ao longo das maiores elevações (Figura 2C). Por fim, um quarto padrão é o de pico em elevações intermediárias, no qual a maior diversidade é observada em elevações intermediárias, enquanto que os menores valores são encontrados nos extremos do gradiente (Figura 2D; McCain, 2009). Destes, o decréscimo linear e o pico em elevações intermediárias são considerados os padrões mais comumente observados (McCain & Grytnes, 2010; Rahbek, 2005). Além disso, o padrão observado depende diretamente do táxon estudado, podendo até mesmo ser observada grande variação nos tipos de padrões de um mesmo grupo taxonômico (e.g. Beck et al., 2017; McCain, 2005). Entretanto, é de extrema importância salientar que, esses quatro padrões, embora mais comuns, não são os únicos passíveis de serem encontrados (Montaño-Centellas et al., 2020).

1.2 PROMOTORES DA DIVERSIDADE

Apesar dos padrões de distribuição de diversidade ao longo dos gradientes ambientais continuarem a ser amplamente estudados, seus mecanismos causais ainda não foram completamente elucidados e continuam sendo fonte de amplos debates (Lomolino, 2001; Graham et al., 2014; Palmer, 1994; Rahbek, 2005). Se considerarmos de forma geral, a distribuição dos organismos pode ser afetada direta e/ou indiretamente por diferentes fatores atuando em múltiplas escalas espaciais e temporais (Graham & Fine, 2008, Levin, 1992). Em grandes escalas, por exemplo, forças evolutivas tais como taxa de especiação e extinção tendem a contribuir mais no processo de criação e manutenção da diversidade (Whittaker et al., 2001). Por exemplo, as regiões tropicais teriam tido mais tempo para que os processos de diversificação pudessem ocorrer, acumulando assim maior número de espécies (Stephens & Wiens, 2003). Por outro lado, desconsiderando o efeito do tempo de especiação, regiões onde as taxas de especiação são elevadas, em conjunto com baixas taxas de extinção, também tendem a ser mais diversas (Smith et al., 2007).

Em escalas menores de espaço e tempo, as interações bióticas, em conjunto com as características ambientais onde as espécies vivem, são considerados fatores que influenciam mais fortemente a diversidade local das assembleias (Graham et al., 2014). Por exemplo, competição, facilitação, parasitismo e predação são interações capazes de regular a diversidade local (Bertness & Callaway, 1994; Paine, 1966; Connell, 1970). Dentre os fatores ambientais conhecidos por influenciar a distribuição das espécies, podemos citar variações na temperatura, precipitação, disponibilidade de alimento, quantidade total de área e habitat disponível, bem como a heterogeneidade ambiental (Brown et al., 2004; Gaston, 2000; MacArthir & Wilson, 1967; Pianka, 1966; Terborgh, 1977).

Além de serem espacialmente variáveis, as comunidades também podem apresentar dinamismo temporal (Chesson & Huntly, 1989; Tonkin et al., 2017). As condições ambientais podem variar anualmente, bem como ao longo de um mesmo ano (i.e., sazonalidade). Tais mudanças podem fazer com que os organismos possam apresentar, por exemplo, sincronismo com a disponibilidade de recursos, condições climáticas favoráveis e baixa pressão de patógenos (McMeans et al., 2015; McNamara & Houston, 2008). Dessa forma, a abundância, diversidade e distribuição das espécies podem estar associadas à essas dinâmicas temporais (Shimadzu et al., 2013; Tompson & Townsend, 1999). Ainda assim, trabalhos que investigam a diversidade ao longo de gradientes ambientais incluindo tais variações temporais são proporcionalmente menos numerosos se comparados àqueles que focam nas questões espaciais (Bishop et al., 2014; White et al., 2010; Willis & Whittaker, 2002).

1.3 O PAPEL DAS MONTANHAS NO ENTENDIMENTO DO PADRÕES E PROCESSOS DE DISTRIBUIÇÃO DA DIVERSIDADE

As montanhas representam 25% da parte terrestre do nosso planeta e seus gradientes de elevação são considerados verdadeiros laboratórios naturais para se investigar como que os mecanismos evolutivos e ecológicos moldam os padrões de diversidade (Körner, 2004; Rahbek et al., 2019). Isso porque, por um lado, é possível observar uma grande variação das condições ambientais em curtas distâncias espaciais (Graham et al., 2014; McCain, 2009). Por outro lado, a diversidade encontrada nesses ambientes pode ser fruto de processos histórico-evolutivos de migração, especiação e extinção derivados de eventos geológicos e climáticos ao longo de milhares e milhões de anos (Rahbek et al., 2019). E além de propiciarem importantes serviços ecossistêmicos para metade da população global (Egan & Price, 2017), os ambientes montanhosos são importantes centros de diversidade, representando metade dos *hotspots* globais de diversidade (Myers et al., 2000; Mittermeier et al., 2011). Estima-se que as montanhas abrigam um terço das espécies terrestres, sendo muitas destas endêmicas de tais regiões (Körner, 2004; Rahbek et al., 2019).

Diversas hipóteses foram levantadas para tentar explicar a variação da diversidade ao longo dos gradientes elevacionais. Variações climáticas e de disponibilidade de área, junto com processos evolutivos e bióticos são os fatores mais utilizados para tentar explicar esses padrões (Gaston, 2000; McCain & Grytnes, 2010). As hipóteses climáticas baseiam-se na mudança contínua das condições abióticas contemporâneas ao longo do gradiente tais como temperatura, precipitação, produtividade e umidade. Esses fatores podem atuar diretamente nos limites fisiológicos dos organismos, restringindo o número de espécies e/ou indivíduos capazes de sobreviver nas diferentes elevações; ou indiretamente, por restringir a produtividade, e como consequência, podendo levar a limitações no número de indivíduos (Brown et al., 2004; Srivastava & Lawton, 1998). Já as hipóteses espaciais baseiam-se na relação espécie-área, uma vez que regiões com maior disponibilidade de área poderiam abrigar um maior número de espécies e/ou indivíduos (Rabek, 1997; Rosenzweig, 1995). Hipóteses que consideram aspectos da história evolutiva predizem a existência de uma região ótima ao longo do gradiente (geralmente em sua base), na qual processos de especiação tenham sido promovidos, enquanto que processes de extinção acabaram sendo atenuados (Lomolino, 2001; McCain, 2009). Processos bióticos tais como aumento da heterogeneidade e complexidade de habitat tendem a promover áreas com maior diversidade, assim como as regiões de ecótonos encontradas nas montanhas (McCain & Beck, 2016; Terborgh, 1977). Já interações biológicas como competição, tenderiam a promover diminuição da diversidade (McCain & Grytnes, 2010).

Estudar os gradientes elevacionais é de extrema relevância haja vista o aumento da destruição e degradação dos ambientes naturais montanos em virtude de ações antrópicas diretas, bem como devido às eminentes consequências das mudanças climáticas globais. (Colwell et al., 2008; Laurance et al., 2011). Essas mudanças vêm acontecendo de forma muito mais rápida nos ambientes montanos, especialmente nas regiões de maior elevação (Nogués-Bravo et al., 2007; Pepin et al., 2015). O aumento generalizado das temperaturas ao longo de todo o planeta tem afetando o limite de distribuição das espécies; muitas delas têm se deslocado para regiões de maiores latitudes, bem como para áreas mais elevadas (Pecl et al., 2017; Sheldon, 2019). E como consequência, espécies restritas às maiores elevações acabam por serem as mais impactadas, uma vez que não teriam mais áreas disponíveis para “subir”, correndo o risco então de acabarem se extinguindo (Freeman et al., 2018).

Estudos buscando entender os padrões e processos por trás da distribuição da diversidade ao longo dos gradientes elevacionais têm se intensificado nas últimas décadas. Entretanto, mesmo com implicações importantes tanto para a ecologia básica quanto para a aplicada (Egan & Price, 2017; Rahbek et al., 2019), trabalhos desenvolvidos especificamente ao longo das montanhas Neotropicais ainda são escassos (e.g. Bañares-de-Dios et al., 2020; Perillo et al., 2021; Siqueira et al., 2021). Tal carência acontece mesmo com a presença de expressivas cadeias de montanhas na região (Figura 3). Dentre estas, destaca-se na porção oeste da América do Sul os Andes, a maior cadeia de montanhas em extensão latitudinal no planeta. Já na porção leste, embora com elevações menos expressivas, diversas cadeias de montanhas podem ser encontradas, principalmente ao longo da Mata Atlântica brasileira (Figura 4).

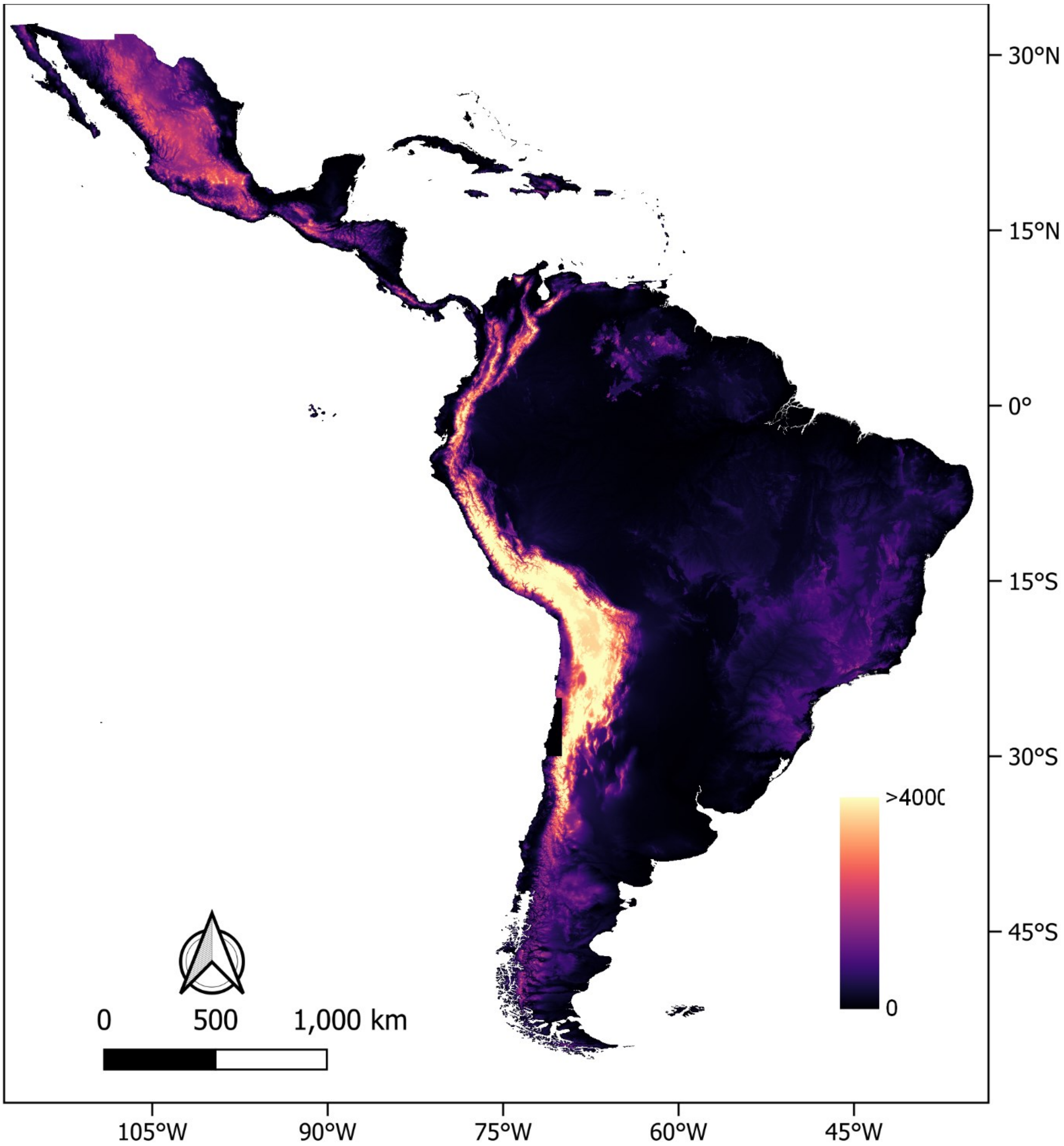

Figura 3. Variação da elevação ao longo da região Neotropical. Mapa gerado a partir de modelo digital de elevação (1 km de resolução) disponibilizado pela U.S. Geological Survey (https://www.usgs.gov).

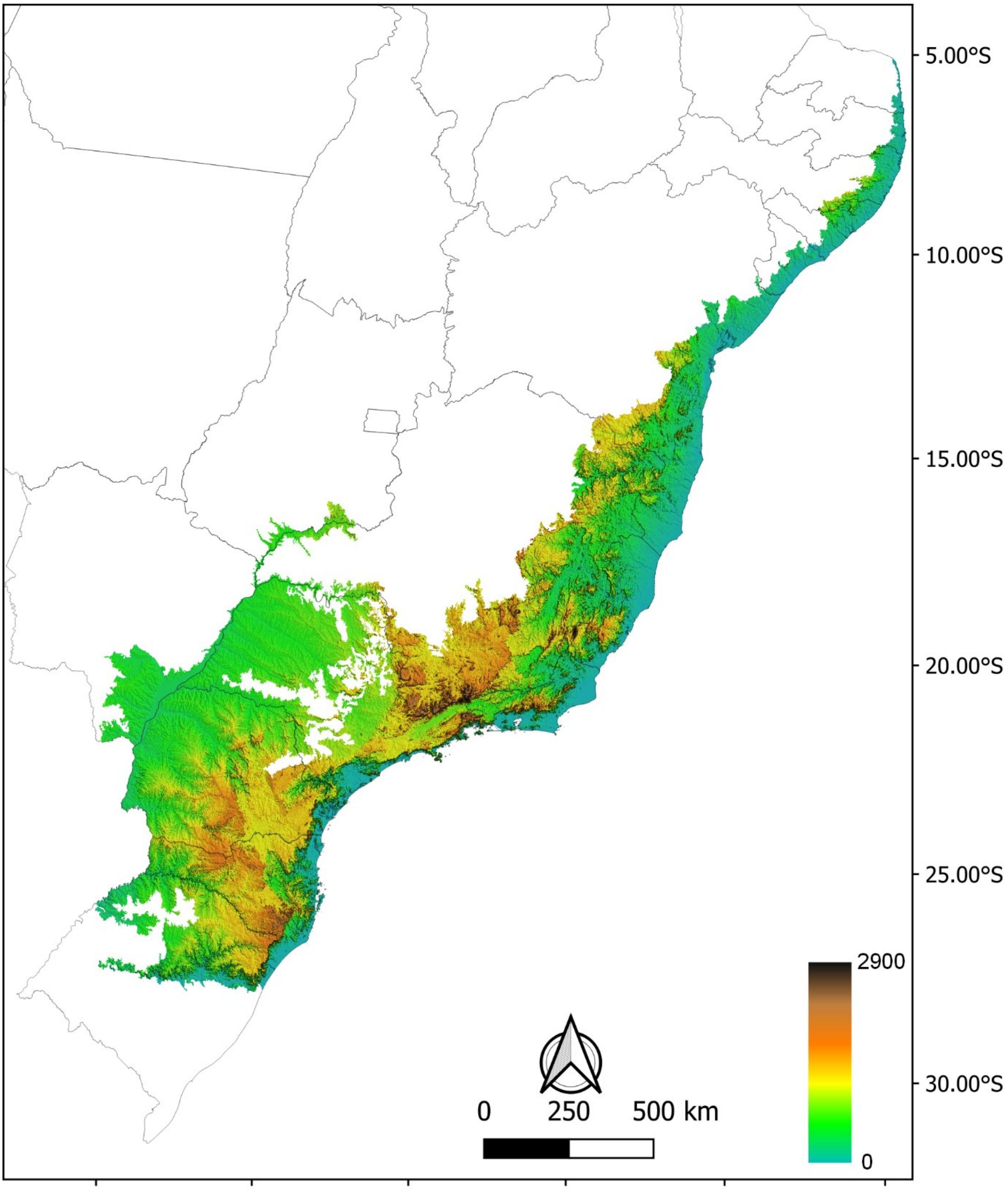

Figura 4. Variação da elevação ao longo do limite da Mata Atlântica Brasileira. Mapa gerado a partir de modelo digital de elevação (30 m de resolução) disponibilizado pela Copernicus Planetary Data Access (https://panda.copernicus.eu).

1.4 A MATA ATLÂNTICA BRASILEIRA E SEUS GRADIENTES ELEVACIONAIS

Com uma grande heterogeneidade topográfica, apresentando desde planícies costeiras a cadeias de montanhas, o bioma Mata Atlântica (MA) estende-se majoritariamente ao longo do litoral brasileiro, sendo encontrada do nordeste ao sul do país, embora também ocorra em pequenas porções do interior do Paraguai e da Argentina (Ribeiro et al., 2009). Apesar de originalmente ter ocupado cerca de 1,5 milhão de km², a MA hoje está reduzida a 28% de sua cobertura vegetal original (Figura 5; Rezende et al., 2018; Ribeiro et al., 2009). Tamanha redução é decorrência de processos crônicos de desmatamento, fragmentação, superexploração de recursos naturais e expansão urbana, no qual esse bioma vem sofrendo ao longo dos últimos cinco séculos (Rezende et al., 2018; Tabarelli et al., 2010). Ainda assim, a MA é considerada uma das regiões mais biodiversas do planeta, apresentando elevado endemismo de plantas, artrópodes, aves e anfíbios (Ströher et al., 2019; Vale et al., 2018; Zappi et al., 2015). Tais características fazem da MA uma das florestas mais ameaçadas a nível global, tornando-a área prioritária de extrema importância para conservação da biodiversidade (Mittermeier et al., 2011; Myers et al., 2000).

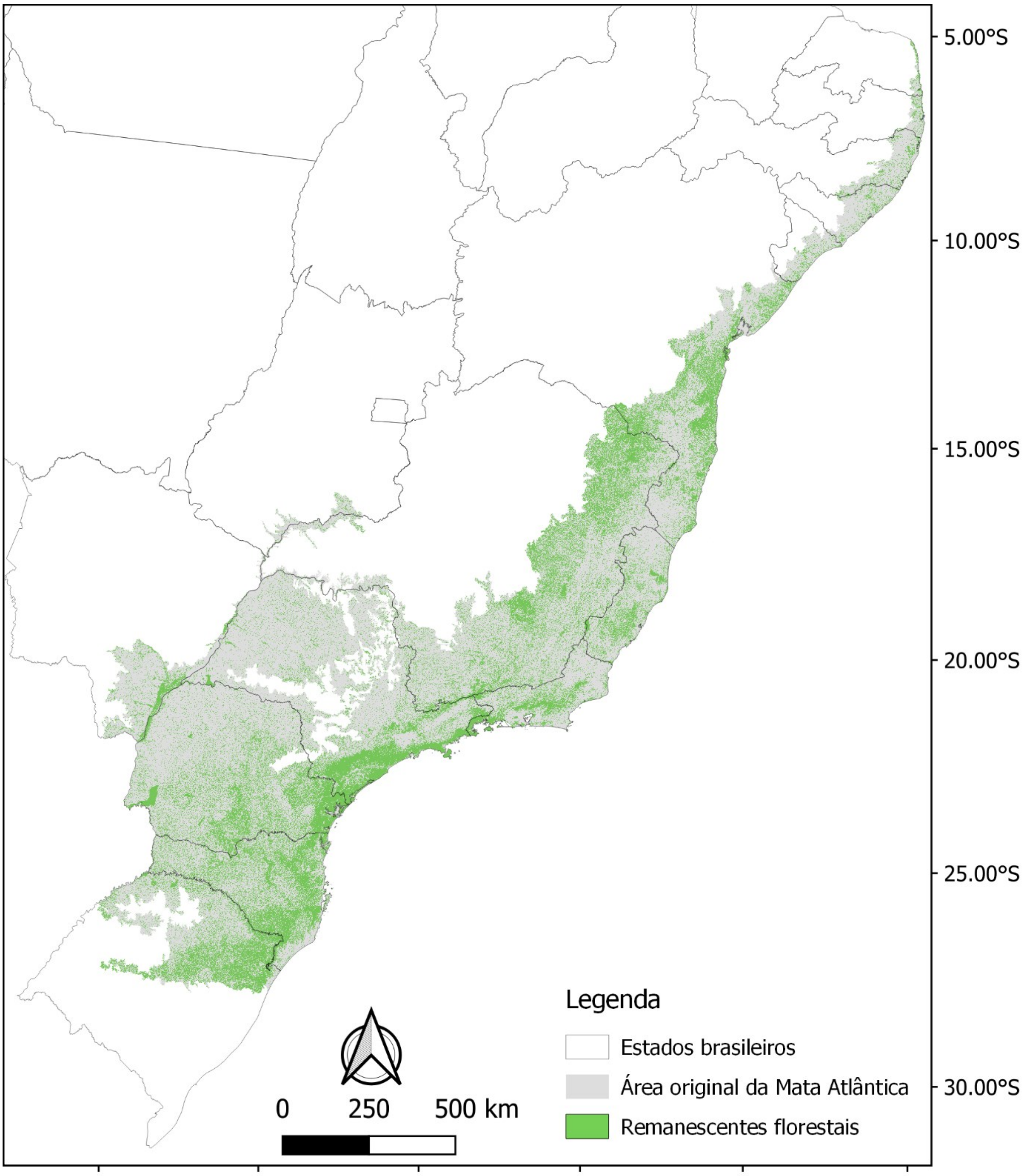

Figura 5. Remanescentes de vegetação nativa ao longo da Mata Atlântica brasileira. Mapa gerado a partir da Coleção 6 da Série Anual de Mapas de Cobertura e Uso de Solo do Brasil, desenvolvida pelo Projeto MapBiomas (https://mapbiomas.org/).

A maioria dos remanescentes de vegetação natural da MA encontram-se fragmentados, apresentando tamanhos inferiores à 50 ha (Ribeiro et al., 2009). Entretanto, grandes extensões florestais ainda podem ser encontradas principalmente ao longo das regiões montanhosas da MA (Figura 5; Tabarelli et al., 2010). Dentre estas, destaca-se a Serra do Mar, formação que se estende do litoral do estado do Rio de Janeiro até Santa Catarina e com elevações que vão de 0 m a 2.366 m, onde cerca de 36,5% de sua cobertura vegetal original ainda persiste (Gonjito-Pascutti et al., 2012; Ribeiro et al., 2011). Outras regiões como a Serra da Mantiqueira e a Formação Serra Geral também apresentam variações expressivas de elevação. A Serra da Mantiqueira, que se estende entre os estados do Espírito Santo, Minas Gerais e Rio de Janeiro, apresenta regiões com até 2.891 m de elevação (Gonjito-Pascutti et al., 2012). Já a Formação Serra Geral, que cobre cerca de 917.000 km² da América do Sul, estendendo-se pelo Brasil desde o estado do Rio Grande a Minas Gerais, contendo áreas que alcançam 1.900 m de elevação (Hartmann, 2014). Apesar de extensivos e diversos, conhecemos muito pouco acerca dos padrões de distribuição da diversidade ao longo dos gradientes elevacionais da MA (e.g., Almeida-Neto et al., 2006; Martinelli, 2007; da Silva et al., 2018).

1.5 ANFÍBIOS COMO MODELO DE ESTUDO

Dentre o grupo dos vertebrados, os anfíbios estão entre os menos estudados nessas regiões montanhosas (McCain & Sanders, 2010; Siqueira & Rocha, 2012). Anfíbios podem ser considerados bons modelos para entendermos os padrões de distribuição da diversidade, bem como seus mecanismos atrelados. Além de apresentarem elevada diversidade (8.442 espécies descritas até o momento; Frost, 2021), os anfíbios são ectotérmicos, possuem pele altamente permeável, dependem de corpos d'água ou locais úmidos para deposição de seus ovos, e apresentam relativamente baixa capacidade dispersiva; fatores estes que os tornam sensíveis às condições ambientais (Duellman & Trueb, 1994; Wells, 2007). Adicionalmente, são o grupo de vertebrados mais ameaçados de extinção a nível global (~41% das espécies estão sob alguma ameaça; IUCN, 2021). Devido às suas características e elevado grau de ameaça, torna imprescindível conhecermos melhor os fatores responsáveis pela distribuição desses animais. Isso porque tais informações são imprescindíveis para subsidiar a criação e o desenvolvimento de estratégias mais eficazes para a conservação dos anfíbios.

E é na Mata Atlântica que encontramos a maior diversidade de anfíbios no Brasil. Pelo menos 625 das 1.188 espécies encontradas em território nacional ocorrem nesse bioma. Destas, 485 (~78%) são consideradas endêmicas (Segalla et al., 2021; Rossa-Feres et al., 2017). Tamanha diversidade é geralmente atribuída à grande variação das condições climáticas e da disponibilidade de microambientes propiciada pela vasta extensão latitudinal (~25°) e complexidade topográfica encontrada ao longo da MA (Figura 4; Haddad & Prado, 2005; Vasconcelos et al., 2019). Mas independentemente de todas essas questões previamente levantadas, são raras as tentativas de se tentar elucidar os padrões de diversidade de anfíbios ao longo dos gradientes elevacionais da MA (e.g., Goyannes-Araujo et al., 2015; Siqueira et al., 2021). Além disso, dos poucos trabalhos que propuseram a abordar esse tema, alguns se restringem a uma pequena porção do gradiente elevacional (e.g., Giaretta et al., 1997; Giaretta et al., 1999), enquanto outros dão mais enfoque na presença das espécies nas cadeias de montanhas em si (e.g., Silva et al., 2018; Neves et al., 2018). Outro fator limitante é a concentração de estudos em regiões montanhosas na porção tropical da MA, como nas Serras do Mar e da Mantiqueira, enquanto que as áreas mais ao sul e de clima subtropical, como as porções da Serra Geral, são praticamente inexploradas. Tamanhas lacunas dificultam então nossa compreensão de como os gradientes elevacionais influenciam nos padrões de distribuição das espécies.

1.6 ESTRUTURA DA TESE

Nesse sentido, essa tese foi construída com a finalidade de se investigar os padrões e processos envolvidos na distribuição da diversidade, bem como na estruturação das assembleias ao longo dos gradientes elevacionais. Para isso, foquei meu trabalho nos anfíbios da ordem Anura de uma região montanhosa localizada na porção subtropical da MA. No Capítulo 1, investiguei o padrão geral de distribuição da diversidade bem como da composição das assembleias de anuros ao longo de um gradiente elevacional. Adicionalmente também avaliei se as características espaciais e ambientais poderiam explicar os padrões observados. No Capítulo 2 investiguei a dinâmica espaço-temporal da diversidade de anuros ao longo desse mesmo gradiente, abordamos duas questões complementares a parti dos resultados obtidos no capítulo 1. Dessa forma, especificamente avaliei o grau de variação sazonal nos padrões de distribuição elevacional da diversidade de anuros, bem como o quanto desses padrões poderiam ser explicados pela variação da temperatura.

2 CAPÍTULO 1 - HABITAT AMOUNT AND AMBIENT TEMPERATURE DICTATE PATTERNS OF ANURAN DIVERSITY ALONG A SUBTROPICAL ELEVATIONAL GRADIENT

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2.1 ABSTRACT

Aim: Patterns of diversity along elevational gradients are driven by species characteristics but remain poorly understood. Filling this gap is imperative given the deteriorating conservation status of anurans worldwide. Here, we examine frog diversity and species composition along a sharp subtropical elevational gradient and assess the degree to which these are determined by environmental and spatial predictors.

Location: An extensive southern Brazilian Atlantic Forest elevational gradient ranging from 300 to 1,800 m above sea level.

Methods: We sampled 38 ponds and used structural equation modelling to examine the direct and indirect effects of area, climate, habitat amount, habitat complexity and productivity on frog species richness and abundance. We also applied joint species distribution models to investigate the importance of these predictors on frog species composition using species distribution and co-occurrence along the elevational gradient.

Results: We recorded 12,636 individuals of 41 frog species. Frog species richness was highest at intermediate elevations, showing a hump-shaped pattern. Frog abundance was highest at lowlands and decreased towards higher elevations. We found support for only the habitat amount hypothesis in explaining overall species richness. Although temperature had a positive influence on productivity and frog abundance, neither predictors were related to species richness. Species composition diverged markedly between lowland and highland frog assemblages, which was mainly attributed to differences in ambient temperature.

Main conclusion: Elevations containing more extensive natural habitat areas retained the most species-rich frog assemblages. The mid-elevational peak is likely attributed to lowland habitat (<800 masl) heterogeneity and extreme climatic conditions in highland areas (>1,400 masl). The entire elevational gradient is, however, critical in maintaining anuran species diversity as lowland assemblages are distinct from those at mid- to high elevations. Our study also shows that anthropogenic habitat loss has a decisive effect on montane frog diversity, reinforcing the need to effectively protect these areas.

Keywords

Atlantic Forest, altitudinal gradient, elevational patterns, environmental filter, frogs, habitat integrity

2.2 INTRODUCTION

Biodiversity heterogeneity along environmental gradients is a central topic in ecology and biogeography (Lomolino, 2001; Ricklefs, 2004). Over the last decades, considerable effort has been allocated to understanding diversity patterns along montane environmental gradients, which correspond to half of all global biodiversity hotspots (Elsen et al., 2018; Körner, 2004). Extensive reviews (e.g. Beck et al., 2017; McCain, 2005, 2010; McCain & Beck, 2016; Rahbek, 2005) and empirical studies on animal and plant communities across montane regions (e.g. Longino & Branstetter, 2018; Zu et al., 2019) recognize four major elevational patterns of species richness: (a) decreasing, (b) low plateau, (c) low plateau with mid-peak and (d) mid-elevation peaks. Nevertheless, the operational spatial scale and the causal mechanisms of these patterns remain unclear (Laiolo et al., 2018; McCain & Grytnes, 2010; McCain et al., 2018).

Proposed explanations generally invoke multiple drivers that can potentially act and interact at different scales (Szewczyk & McCain, 2019; Willing & Presley, 2016). Variation in contemporary climatic conditions, such as temperature and precipitation, may directly filter out organisms given their physiological tolerance, leading to changes in species richness and composition (i.e. a positive climate-diversity relationship; Fu et al., 2006; McCain, 2009). Warmer climates mostly lead to higher primary productivity, resulting in more available resources, which in turn ensure coexistence of more individuals (McCain, 2007). Therefore, productivity can indirectly promote diversity by maintaining more viable populations and reducing local extinction rates, also known as the more-individuals-hypothesis (MIH: Binkenstein et al., 2018; Srivastava & Lawton, 1998). Diversity also scales to the available habitat area, and montane regions covering larger areas or providing more available habitat should also harbour more species and individuals (Fahrig, 2013; Rosenzweig, 1995). This area-diversity relationship is based on the assumption that larger habitat areas reduce extinction rates and are more likely to encompass more habitat types (MacArthur & Wilson, 1967; Rosenzweig, 1995). Biotic processes such as competition, habitat complexity and habitat heterogeneity across ecotones have also been proposed to explain elevational patterns of diversity (Beck et al., 2017; McCain & Beck, 2016; McCain et al., 2018). However, the contribution of these factors to montane diversity remains unclear given the difficulty in measuring these processes along natural elevational gradients.

Montane regions of the Brazilian Atlantic Forest biome (hereafter, AF) harbour a remarkable diversity of endemic plants, arthropods, birds and frogs (e.g. Garey & Provet, 2016; Vale et al., 2018). However, the AF is a highly threatened global biodiversity hotspot with only 26% of its original forest cover remaining, most of which scattered across thousands of fragments <50 ha (Rezende et al., 2018; Ribeiro et al., 2009). Virtually all extensive tracts of AF are in montane regions, rendering them a conservation priority (Tabarelli et al., 2010). However, there have been few attempts to elucidate the elevational patterns of diversity throughout the AF (e.g. Almeida-Neto et al., 2006; Martinelli, 2007; da Silva et al., 2018).

Atlantic Forest anurans are especially diverse, with 625 recorded species, 85% of which are endemics (Rossa-Feres et al., 2017). This high level of diversity has been attributed to the exceptional heterogeneity of macro- and microhabitats, topography and climatic variation across this biome (Brown & Brown, 1992; Haddad & Prado, 2005). However, this frog diversity is threatened by the relentless impacts of habitat fragmentation, habitat loss, climate change and infectious diseases, all of which elevate anurans to the most threatened vertebrate taxon worldwide (Becker et al., 2007; IUCN, 2019; Stuart et al., 2004). Despite the vast remaining extent of montane AF habitat, investigations on the variation in frog diversity along elevational gradients remain scant, and available data are restricted to a few sites and narrow elevational ranges (350-750 masl; Giaretta et al., 1997; Giaretta et al., 1999; Goyannes-Araújo et al., 2015). Given the rapid pace of habitat conversion and degradation, basic information on AF frog diversity is therefore crucial to help develop evidence-based conservation strategies (Pereira et al., 2013).

Here, we investigate the patterns and potential drivers of frog diversity along an extensive subtropical elevational gradient in the southern Atlantic Forest. First, we describe how frog species richness and abundance changes with elevation. We expected mid-elevation peaks in frog diversity, which is consistent with the trend for all major vertebrate taxa (McCain & Grytnes, 2010). Second, we assess the role of environmental and spatial variables on frog species richness and abundance by simultaneously testing predictions from six major hypotheses of diversity: area, climate, habitat complexity, habitat amount, MIH and productivity (Table 1). Finally, we describe the compositional variation in frog assemblages along the elevational gradient and assess the contribution of environmental predictors and species relationships on the structure of these assemblages.

Table 1 Major hypotheses and predictors of frog diversity along elevational gradients considered in this study.

Hypothesis	Theory	Predictor	Scale
Area	Diversity is positively related to area (MacArthur & Wilson 1967; Rosenzweig, 1995)	Pond surface area (PSA)	Local
		Elevational band area (Area)	Landscape
Climate	Diversity is positively related to temperature (Allen, Brown & Gillooly, 2002)	Mean annual temperature (MAT)	Landscape
Habitat complexity	Diversity is positively related to habitat complexity (Rosenzweig, 1995)	Water surface cover (WSC)	Local
		Pond vegetation structure (PVS)	Local
Habitat amount	Diversity is positively related to total habitat amount (Fahrig, 2013)	Pond habitat amount (PHA)	Local
		Band habitat amount (BHA)	Landscape
More-individuals-hypothesis	Abundance is positively related to productivity, and therefore species richness is positively related to abundance (Binkenstein et al., 2018; Srivastava & Lawton, 1998)	Frog abundance	Local
Productivity	Diversity is positively related to productivity (McCain, 2009)	Net primary productivity (NPP)	Landscape

2.3 METHODS

2.3.1 Study area

The largest remaining AF montane forest habitat span the Serra do Mar, Serra da Mantiqueira and Serra Geral ridges of south-eastern and southern Brazil, where elevations range from sea level to ~2,900 m (Gontijo-Pascutti et al., 2012). This study was carried out within the Serra Geral, a complex montane landscape formed mainly by Early Cretaceous lava flows, which are associated with the break-up of Gondwana, separating the modern continents of South America and Africa (Hartmann, 2014). The ~920,000 km² Serra Geral region extends from Argentina through Uruguay, Paraguay and southern to south-eastern Brazil (Frank et al., 2009). Specifically, we focused on the ~49,800 ha São Joaquim National Park (hereafter, SJNP), a strictly protected area located in the state of Santa Catarina, Brazil (Figure 1). The study area spans approximately 1,200 km² of dissected terrain and altitudes ranging from 200 to 1,822 masl (Vianna et al., 2015). The vegetation comprises of a mosaic of dense evergreen forest largely occurring up to 800 masl, replaced by mixed Araucaria forest and high-altitude grasslands at higher altitudes (IBGE, 2012). The climate is humid subtropical without a dry season with some variation depending on elevation: hot summers and mean annual temperature of 19°C below 800 masl, and cold winters with frequent frosts and a mean annual temperature of 13.5°C above 800 masl (Alvares et al., 2014).

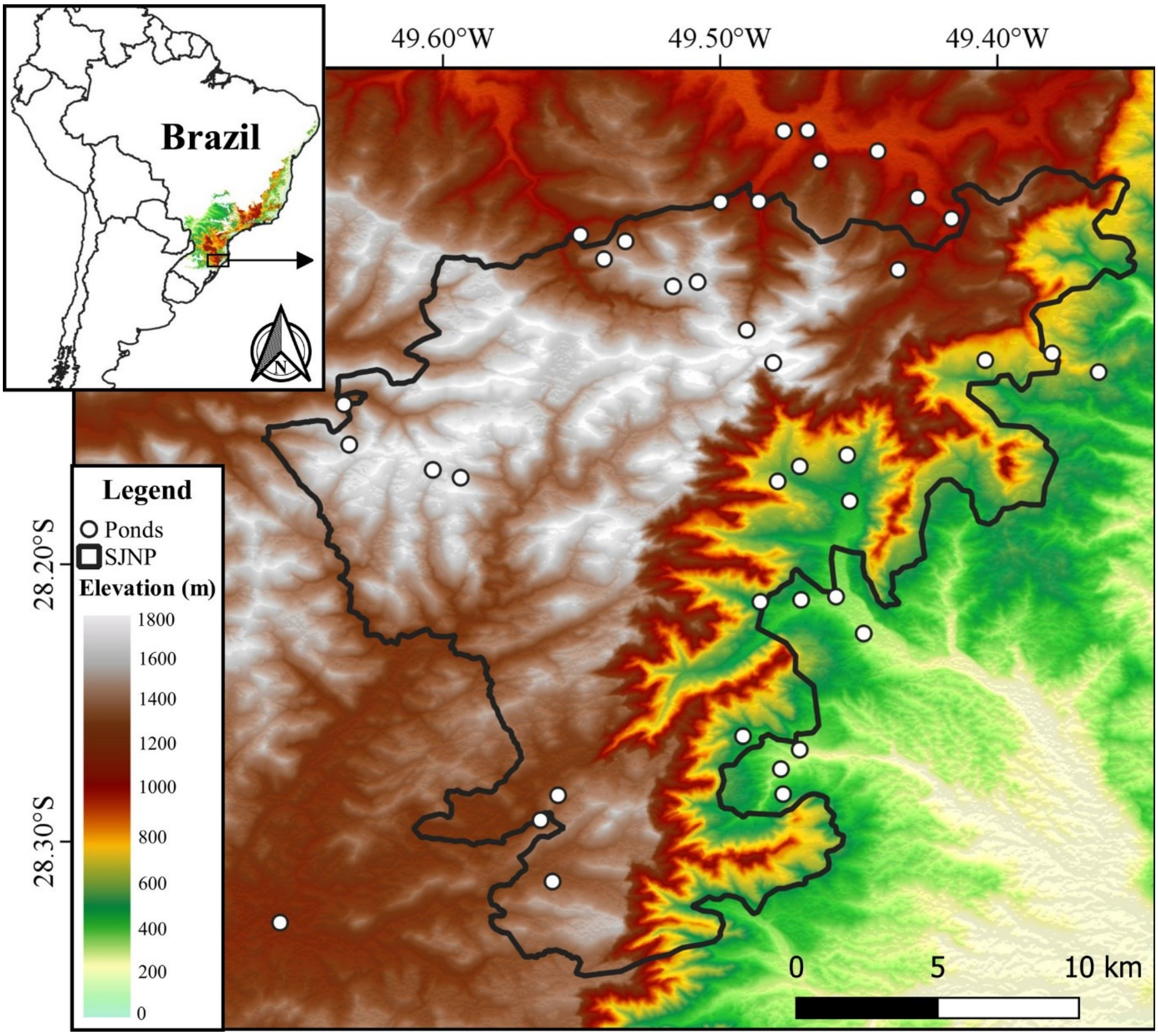

Figure 1. Altitudinal variation of the Brazilian Atlantic Forest, showing the study region of the ~49,800-ha São Joaquim National Park (SJNP) and surrounding areas within the state of Santa Catarina, Brazil (inset map). Open circles indicate the location of the 38 perennial ponds surveyed in this study.

2.3.2 Sampling design

We sampled frogs along 38 discrete lentic aquatic environments (ponds, humid areas, marshes and small dams; hereafter, ponds) located between 312 and 1796 masl (Figure 1). We acknowledge that some specialist anuran species (i.e. ground-dwelling, stream-dwelling and bromeliad breeders) may have been undersampled, but ponds are considered suitable environments given that most AF frogs use them and their vicinities to reproduce and forage (Crump, 2015; Haddad et al., 2013). We employed the following steps to select survey ponds. We first subdivided the elevational gradient into eight 200-m elevational bands, from 200 to 1,800 masl, which ensured that pond selection was not biased for or against any single region of the elevational gradient (McCain & Grytnes, 2010). Using a complete map of all water bodies recorded for the state of Santa Catarina (SIGSC; available at http://sigsc.sc.gov.br/sigaresc/), we searched for all perennial ponds within these bands, but up to 5 km from the boundaries of SJNP, corresponding to a planimetric area of ~7,854 km2. The SIGSC contains spatially accurate geographic and elevational data derived from 70,000 high-resolution aerial photographs of the State of Santa Catarina (year 2012). We further validated pond locations based on the Shuttle Radar Topography Mission (SRTM) elevational data with 30-m or 1 arc-sec spatial resolution (Valeriano & Rossetti, 2012). We randomly selected five ponds for each elevational band that (a) were at least 1 km apart; (b) were surrounded by negligible anthropogenic habitat disturbance; and (c) were no farther than 5 km from the nearest access road. Prior to sampling, we visited all selected ponds to confirm their presence and accessibility. Due to restricted availability, only four ponds were selected between 1,000 and 1,200 masl and between 1,600 and 1,800 masl. A detailed description of each pond can be found in Appendix S1.1 in Supporting Information.

2.3.3 Frog survey

We quantified frog species richness and abundance at each pond based on 10 monthly samples from September 2017 to August 2018, except for December 2017 and April 2018. We combined visual and acoustic encounter surveys, within a 5-m buffer along the pond perimeter and recorded all frogs on the water surface, above and underneath any vegetation, rocks and logs (Scott-Jr & Woodward, 1994). A 5-m survey buffer was selected do maximize visual and acoustic anuran detectability, avoiding double counting. Sampling initiated at least one hour after dusk (17:30 hr-19:18 hr) and ended no later than 01:00 hr. Sampling effort was standardized by one person-hour per pond per month. Each pond therefore accumulated a sampling effort of 10 person-hours, amounting to an overall effort of 380 person-hours of active search time. Up to four ponds were surveyed each night, and the pond survey sequence was randomized across months to minimize any bias related to nocturnal sampling schedules. We collected two voucher individuals per species per pond using a research permit previously granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, permit #59223-1). All vouchers were deposited at the Herpetological Collection of the Universidade Federal de Santa Catarina (CHUFSC), Brazil.

2.3.4 Environmental and spatial predictors

We measured environmental and spatial variables at both local and landscape scale. Ponds and their immediate surroundings (within a 500-m radial buffer) were defined as the local scale. At the landscape scale, we opted for a different approach from most previous altitudinal gradient studies because our sampling protocol was not restricted to a single survey site per evenly spaced elevational band. We therefore followed Peters et al. (2016) in quantifying predictors at the landscape scale and considered the entire area within an elevation range of + 50 m above and –50 m below the elevation centroid of each pond. This approach mirrors the 100-m elevation band typically used in elevational gradient studies (McCain & Beck, 2016; McCain & Grytnes, 2010). We hereafter refer to the landscape scale as the elevational band. Additionally, boundaries of elevational bands were delimited by the 50-km radius from the highest mountain top across the entire study region as suggested by McCain (2007).

Habitat complexity was measured at the local scale, using two widely used proxies based on previous studies on neotropical frog diversity (e.g. Melchior et al., 2017; da Silva et al., 2012). The first was the proportion of pond water surface covered by aquatic and/or emergent vegetation (WSC). The second was the proportion of pond margins covered by shrubs and/or trees, which we used as a proxy of pond vegetation structure (PVS), with higher values indicating more complex habitats. WSC and PVS values were determined using aerial photographs (summer 2018) taken by a rotary-wing drone (Phantom 3 Standard, DJI, China) and subsequently analysed using the ImageJ software (Rasband, 1997). Habitat amount was considered as the percentage of natural vegetation cover measured at both the pond (PHA) and the elevational band (BHA) scales. We included these predictors because even though SJNP is a protected area, private agricultural landholdings are still active inside the park boundaries. Additionally, some ponds were also located outside the SJNP area and had been exposed to some anthropogenic activities. PHA and BHA values were obtained using previously classified, georeferenced 30-m resolution land cover data available from MapBiomas, the Brazilian

Annual Land Use and Land Cover Mapping Project (collection 3.1; year 2017; http://mapbiomas.org/).

Pond water surface area (PSA) was defined as a local area predictor and measured in the field using a GPS Garmin Oregon 550® considering the maximum flood level. Total area of elevational bands was calculated using the SRTM 30-m digital elevation model available in TOPODATA (http://www.dsr.inpe.br/topodata). We used mean annual temperature (MAT), mean observed temperature during surveys (MOT) and mean annual cumulative precipitation (MAP) as proxies of contemporary climatic conditions. Values of MAT and MAP were extracted from the WorldClim database (~1 km^2 spatial resolution; 1970-2000 temporal resolution; Fick & Hijmans, 2017). Ambient temperature was measure at the beginning and at the end of each survey at each pond using an Inconterm 7,664® digital thermometer. As a measure of ecosystem productivity, we extracted the mean net primary productivity (NPP) estimates produced by the moderate resolution imaging spectroradiometer (MODIS) monthly product (MOD17A3; 30 arc-sec or ~1-km^2 resolution temporal extent 2000-2015; http://www.ntsg.umt.edu/project/modis/mod17.php). MAT, MAP and NPP were calculated by averaging values within each elevational band, and values of MOT were calculated by averaging values across all 10 monthly surveys.

All GIS analyses were performed using the Albers Equal Area Conic projection in QGIS v3.4 (QGIS Development Team, 2019). Hydroperiod was not considered because only four of the 38 ponds became almost dry in three of the 10 sampling sessions. We do not include predictions concerning the mid-domain effect because the lower boundaries of our study landscape are not constrained, and species ranges could extend for over 70 km to the eastern coastline (Rana et al., 2019).

2.3.5 Data analysis

Species were assumed to occur at all elevations between the lowest and highest elevations at which they were detected, a common range interpolation approach in elevational gradient studies (Rowe & Lidgard, 2009). This can be considered the most realistic approach to understand diversity patterns as species tend to be distributed continuously (Rowe & Lidgard, 2009). We also used total species richness and abundance based on all surveys at each pond, given that overall sampling effort was equal at each pond. We acknowledge that local diversity may change through time and data pooling may lead to overestimated species richness and abundance. However, few individuals are usually found more than once in a reproductive event, which is associated with the generally low recapture rates within year compared to between years (e.g. Nomura et al., 2012; Tucker, 1995). Therefore, we considered this a valid approach in representing frog diversity at the pond scale, and any temporal variation in frog diversity will be investigated elsewhere.

We assessed our data reliability by evaluating sample completeness by means of sample coverage (Chao et al., 2014). We also estimated asymptotic species richness using the species abundance data at each pond using the iNEXT R package (Hsieh et al., 2016). We then used Pearson correlations to examine observed and estimated species richness values.

Prior to analysis, we examined a predictor correlation matrix to reduce issues of multicollinearity. Mean annual temperature, observed temperature and precipitation were highly correlated (Pearson r = +0.93, –0.98 and –0.90, respectively; Appendix S2.1) so we opted to retain the former as a proxy of climatic conditions. Precipitation values are relatively high along the SJNP elevational gradient (range = 1,463-1,817 mm/yr; see Appendix S1.1 for predictor values along the elevational gradient), and given the marked precipitation aseasonality (absence of a dry season), we assumed that rainwater is not a limiting factor in the study region. Additionally, MAT was also highly negatively correlated with PHA and BHA (r = –0.75 and r = –0.81, respectively; Appendix S2.1), but we opted to retain MAT and both habitat amount variables in order to assess the purposed hypotheses.

We examined the distribution of frog species richness and abundance along the elevational gradient using generalized additive models (GAMs), which incorporate more flexible smoothing functions in modelling nonlinear relationships compared to generalized linear models (Hastie & Tibshirani, 1990). We used a thin plate regression spline on elevation, set the data family to Poisson for richness and negative binomial for abundance (to account for overdispersion) and allowed scaling parameters to be estimated in model fitting. Smoothing parameters were estimated using restricted maximum likelihood (REML) and basis dimension (k) set to five to prevent overparameterization (Peters et al., 2016). GAMs were computed using the mgcv R package (Wood, 2011). The presence of any residual spatial autocorrelation in both species richness and abundance was tested using Moran's eigenvector maps based on 42 different spatial weighting matrices (Bauman et al., 2018), but none could be found (see details in Appendix S3).

We used structural equation modelling (SEM; Grace, 2006) to simultaneously test the direct and indirect effects of multiple hypothesized predictors of frog species richness and abundance. SEM constructs a network of causal relationships, where pathways and their directions indicate previously formulated hypotheses (Grace et al., 2010). Using this framework, we developed an initial full model encompassing the hypothetical a priori causal relationships among the measured predictors and response variables (Appendix S4.2). First, we hypothesized that productivity (NPP) would be directly and positively influenced by temperature (MAT). We would also expect that frog abundance was directly influenced positively by habitat complexity (WSC and PVS), area (PSA and Area), habitat amount (PHA and BHA) and productivity, but also via a direct or indirect effect of temperature (mediated by productivity). Lastly, we expected that these same predictors would directly influence positively frog species richness, but also indirectly, via indirect abundance-mediated effects.

SEM was applied in a Bayesian framework with local estimation of parameters to account for specific error distribution on each response variable using the brms R package (Carpenter et al., 2017). Therefore, productivity, abundance and species richness were modelled with gamma, negative binomial and Poisson error distribution (all log link), respectively. For each model, we ran four chains with 50,000 iterations each, with the first 25,000 discarded as burn-in and the remaining thinned by 100, so that 1,000 samples from the posterior distributions were retained for analysis. We used brms default weekly informative priors for parameters estimate (Lemoine, 2019). Chains convergence was assessed by ensuring that potential scale reduction factor (Rhat) values were less than or equal to 1.01 for all parameters (Bürkner, 2017). We considered relationships important when predictors' highest 95% posterior density intervals (HPDIs) exclude zero. In addition to raw estimates, we also computed paths coefficients standardized on relative ranges (Grace et al., 2018) and calculated the Bayesian R2 for each response variable (Gelman et al., 2019).

Classic approaches to analyse multivariate species data do not account for proper mean-variance relationships of abundance, nor provide sufficient quantitative information on the contributions of different community assembly processes, which may lead to misleading interpretations (Hui et al., 2015; Warton et al., 2012). Therefore, we employed a joint species distribution model (JSDM; Pollock et al., 2014) with the inclusion of latent variables (LVs) to simultaneously describe the pattern of compositional variation and estimate the contribution of predictors on assembly processes. JSDMs extend multivariate generalized linear models by using LVs, which ensure separating species co-occurrences given (dis)similar responses to known environmental predictors (e.g. environmental filtering), to unexplained species associations ("residual correlation"; Ovaskainen et al., 2017; Warton et al., 2015). These residual correlations can either represent responses to unmeasured predictors or the outcome of biotic interactions (D'Amen et al., 2018; Warton et al., 2015).

We fitted JSDMs using the boral R package (Hui, 2016), which uses Bayesian Markov chain Monte Carlo (MCMC) sampling to estimate model parameters. First, we fitted a pure latent variable model (LVM) including only two LVs, which can be understood as a model-based unconstrained ordination (Hui et al., 2015; Warton et al., 2015). From this model, we extracted the posterior median LVs values and used as unconstrained ordination axis coordinates to visualize the variation in species composition across ponds. We then fitted a second model by adding the same covariates used to model species richness and abundance (MAT, NPP, BHA, PHA, PVS, Area, WSC and PSA), but also included vegetation type (either dense evergreen forest or mixed Araucaria forest) where ponds were located, plus two LVs. We also extracted the posterior median LVs values to visualize pond-scale species composition after controlling for environmental predictors (residual ordination). We then quantified correlations in frog species' abundance due to shared environmental responses and their respective residual correlations (responses to unknown covariates or biotic interactions) (Ovaskainen et al., 2016; Warton et al., 2015). Lastly, we performed variation partitioning among the included predictors to quantify their relative contribution in structuring frog assemblages (Ovaskainen et al., 2017).

Predictors were centred and standardized prior to inclusion into JSDMs. For this analysis, we only included species that occurred in at least three ponds to avoid misinterpretations (n = 28; Warton et al., 2015). We ran models using the default uninformative normal priors for model parameters. The number of iterations on MCMC chains was set to 200,000 with a 100,000 burn-in period and a thinning factor of 100. A negative binomial error distribution was used to account for overdispersion in modelling species abundance simultaneously. We also included a site random effect to account for any possible spatial autocorrelation (Hui, 2016). Model convergence was assessed using a combination of the Geweke diagnostic (Geweke, 1992) and visualization of trace plots, while Dunn-Smyth residuals plots were used to inspect violation of model assumptions (Hui, 2016). Correlations were considered important whenever their corresponding 95% HPDIs excluded zero.

2.4 RESULTS

We recorded a total of 12,636 frogs across the 38 surveyed ponds, representing 41 species and nine families (Appendix S5.3). Some species, such as *Boana bischoffi* (n = 3,022 individuals), *Leptodactylus latrans* (n = 1,357) and *Sphaenorhynchus surdus* (n = 353), virtually occurred along the entire elevational gradient (Figure 2). In contrast, *Scinax tymbamirim* (n = 801) and *Phyllomedusa distincta* (n = 97) were restricted to lowland ponds (<800 m), whereas *Boana joaquini* (n = 209) and *Scinax squalirostris* (n = 52) were only found at high-elevation ponds (>800 m) (Figure 2). We also recorded 10 individuals of the alien bullfrog species

Lithobates catesbeianus, all of which within a single pond at 1,139 masl, but these were excluded from subsequent analyses.

Frog species richness showed a hump-shaped pattern at intermediate elevations (Figure 3a). We observed a maximum richness peak at around 620 masl (25 species), followed by similarly high values up to ~1,450 masl, where numbers of species began to decrease until the highest altitudes (deviance explained = 81.8%, $p < .001$; Figure 3a). Frog abundance showed the highest levels at low altitudes, with a maximum at around 320 masl (919 individuals), followed by a monotonic decrease through high elevations (DE = 30.7%, $p < .001$; Figure 3b). Estimated and observed species richness were highly correlated ($r = 0.94$, $p < .001$), and sample coverage values indicated sufficient sampling effort and reliability in our estimates (all values ≥ 0.95; Appendix S6.4).

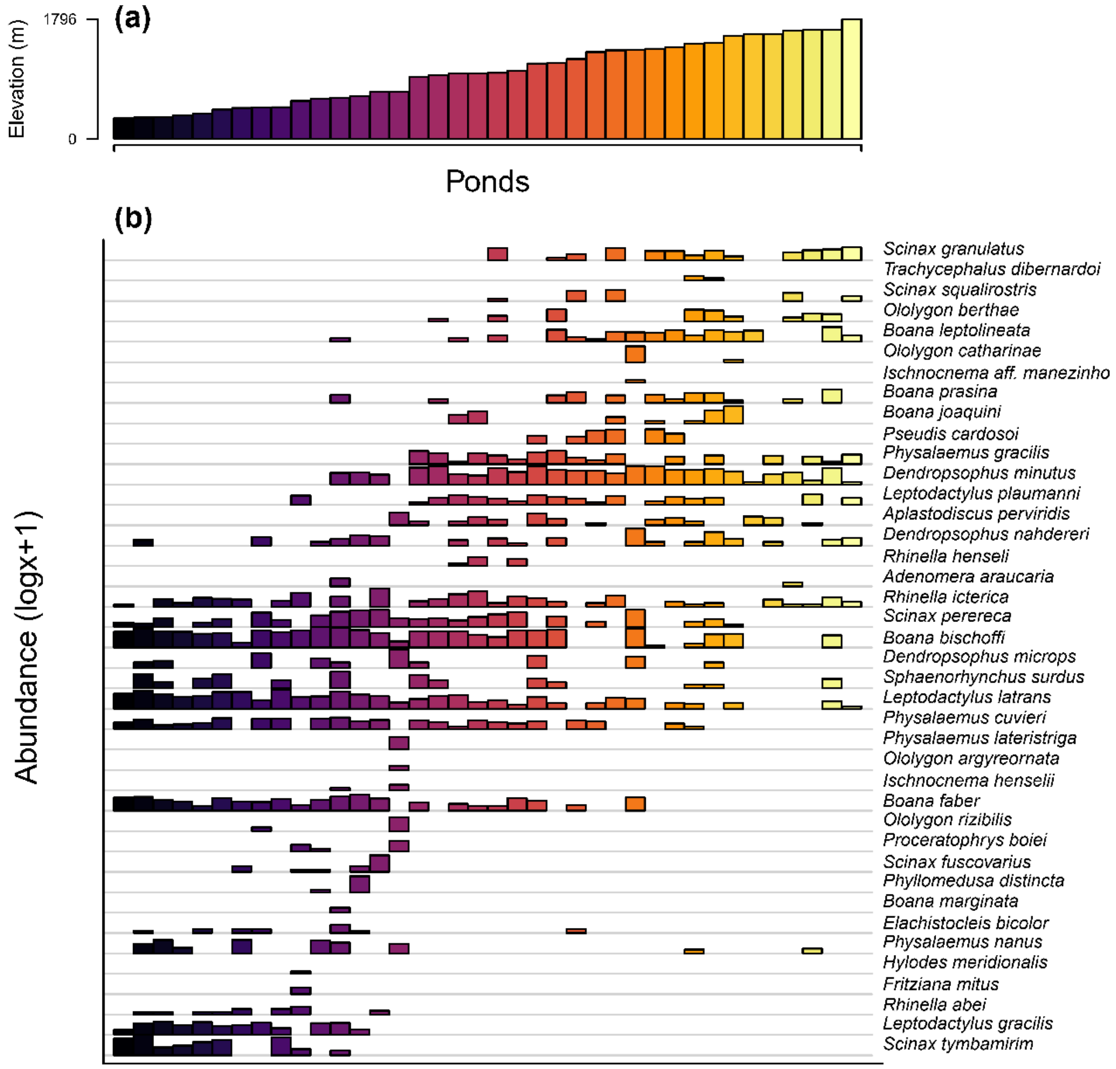

Figure 2. Anuran occurrence and population abundance in perennial ponds distributed along the entire SJNP elevational gradient and surrounding areas in the state of Santa Catarina, Brazil. (a) Upper panel shows the elevation distribution of ponds, and (b) lower panel shows the observed species abundance (log x + 1 for better visualization) at each pond.

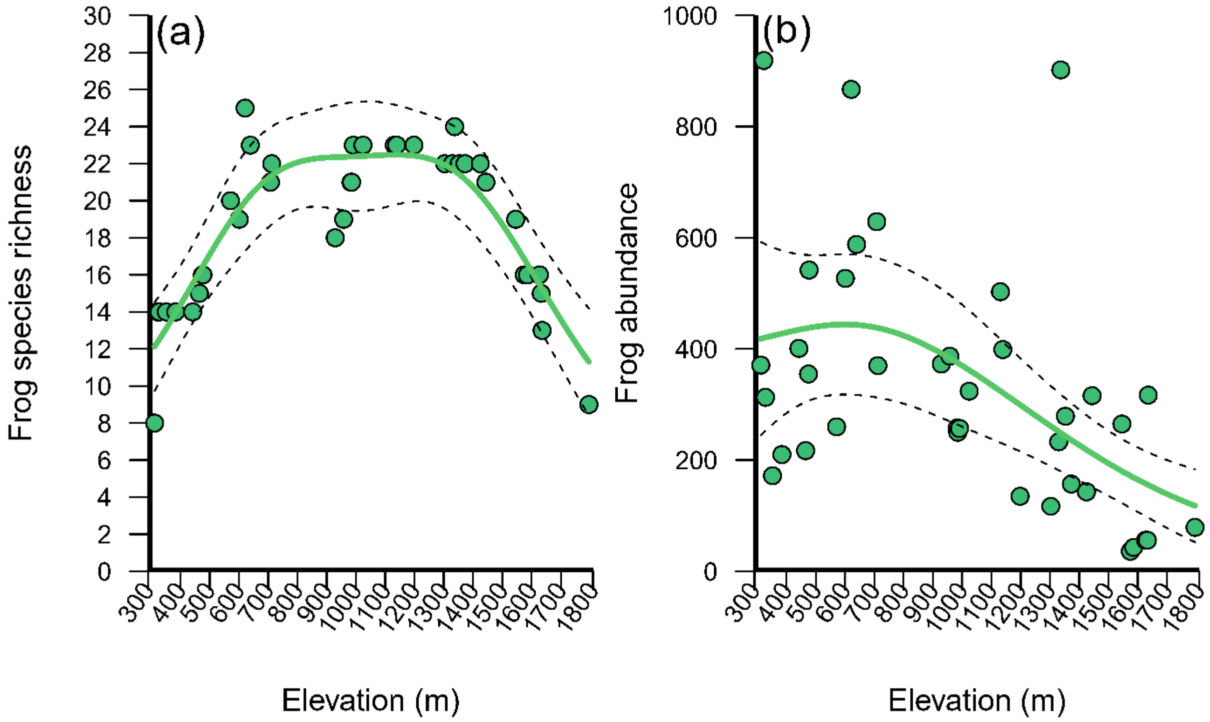

Figure 3. Patterns of (a) frog species richness and (b) abundance along the elevational gradient at SJNP and surrounding areas. Dots represent values for each of the 38 ponds. Solid lines represent trends and dashed lines the respective 95% credible intervals computed using a generalized additive model.

In the mechanistic SEM proposed with the direct effects of temperature, productivity, area, habitat amount and habitat complexity on frog species richness, plus their indirect effects though frog abundance, only the proportion of natural habitat remnants within elevational bands (BHA) was considered an important predictor of richness (i.e. 95% HPDIs excluded zero; Figure 4). Standardized path coefficient indicates that local frog species richness increases in 45% of its observed range values when moving from areas with minimum to maximum BHA (observed range: 57% - 99%). Similarly, mean annual temperature (MAT) was the only important predictor of frog abundance (Figure 4). Moving from colder to hotter areas (range: 11.7°C - 18.5°C), frog abundance increases by 43% of its observed range. Lastly, even though we found that mean annual temperature positively influences net primary productivity, our data provide no support for the more-individuals-hypothesis. Neither the direct nor indirect effect of productivity through abundance was important in predicting local frog species richness. Predictors´ raw path coefficient estimates, HPDIs, convergence and estimated sample size can be found in Appendix S7.5.

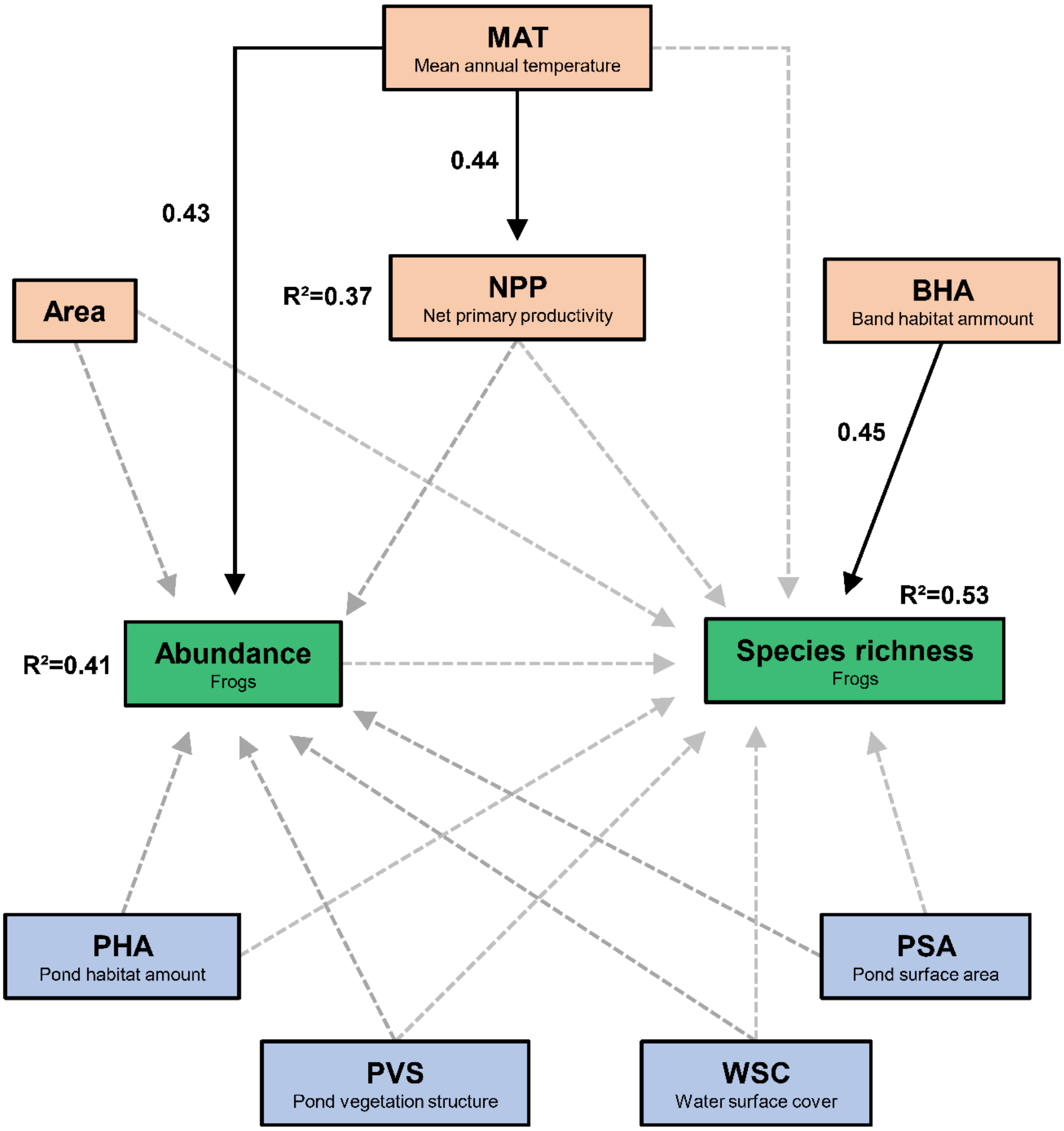

Figure 4. Path models showing the direct and indirect effects of hypothesized predictor variables on frog species richness and abundance along the SJNP elevational gradient and surrounding areas. Important (i.e. 95% high posterior density interval exclude zeros) and unimportant predictors are depicted with solid and dashed arrows, respectively. Numbers on path arrows represent relevant range standardization coefficients for important predictors and the relative amount of prediction capacity (Bayesian R2) is given for response variables. All relationships were hypothesized to be positive.

Pond sites showed a clear elevational gradient in species composition (Figure 5a). The unconstrained ordination showed a separation along the second latent variable axis, with a tight cluster of ponds at the bottom left and another sparser cluster spanning the top along the first latent variable. The first cluster was formed mainly by ponds at lower elevations (300-800 masl), whereas the second consisted of mid- to high-elevation ponds (>800-1,800 masl), thereby reflecting the observed altitudinal gradient (Figure 5a). The residual ordination indicates that most of the variability among ponds were no longer detected once the environmental predictors were included (Figure 5b). Therefore, it was not possible to identify any distinct clusters based on elevational differences, but a few ponds remained more segregated from the core of the ordination (Figure 5b).

We detected both positive and negative important correlations (i.e. 95% HPDIs exclude zero; n = 106) due to similar responses to measured predictors for several species (Figure 5c), indicating that environmental filtering was important in producing correlations in species abundance. Of these, 57% were positive (n = 60) and 43% (n = 46) were negative, indicating that observed correlations in species abundance were mostly attributed to convergences rather than divergences in species-specific responses to predictors. In contrast, we observed a greatly reduced small set of important residual correlations after accounting for environmental predictors (n = 16), all of which were positive (Figure 5d). The joint species distribution model indicated that all measured predictors combined accounted for 77% of the variation in species abundance (averaged over species; Figure 5e). Of these, mean annual temperature was most influential in frog species composition, as on average 22% of the variance in species abundance was attributed to this covariate (Figure 5e). Other predictors contributed individually to less than 10% of the variance.

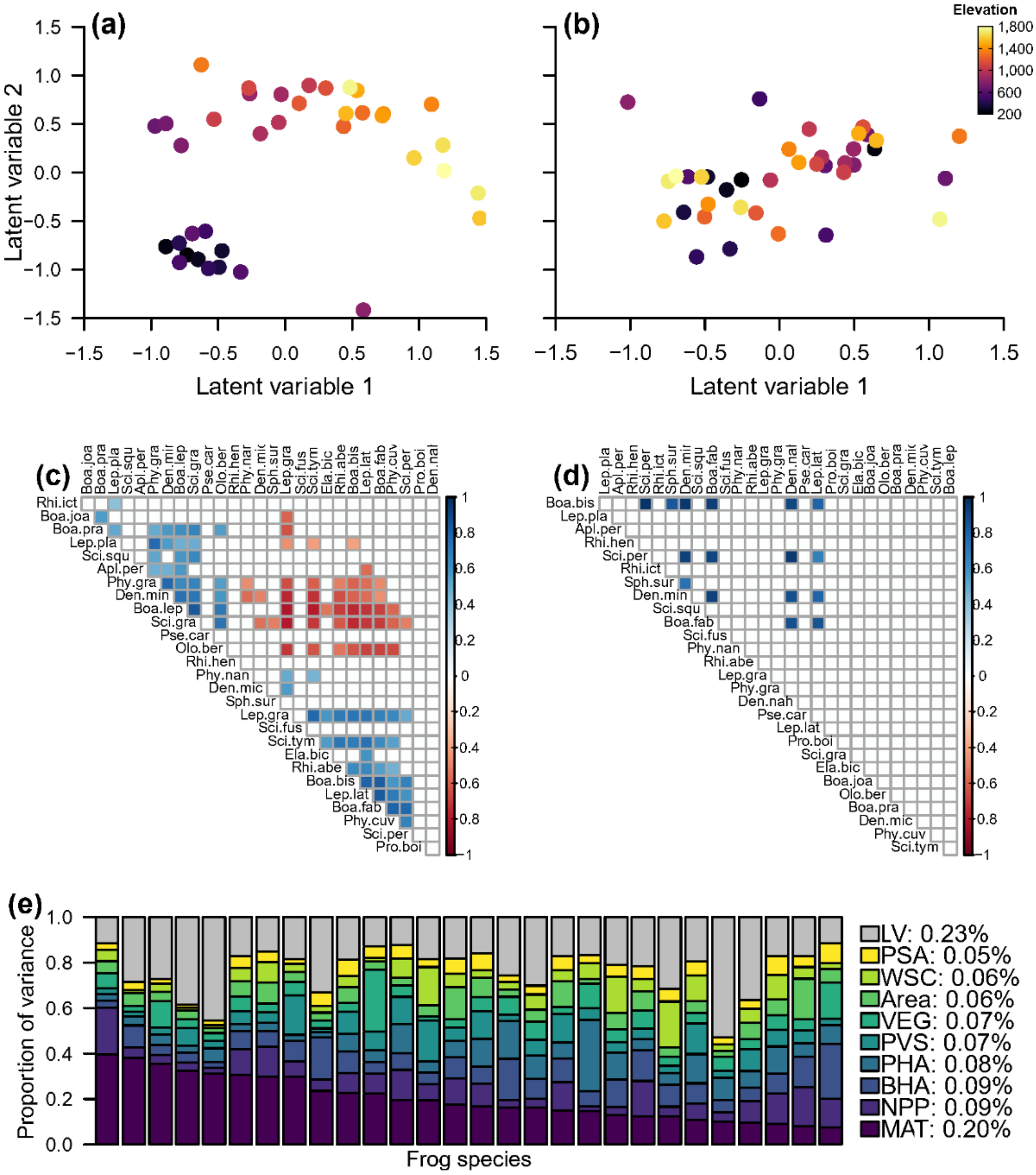

Figure 5. Influence of predictors on the community composition, species correlation and variation in frog species abundance within ponds along the SJNP elevational gradient, Santa Catarina, Brazil. The first two panels show (a) the model-based unconstrained ordination based on the pure latent variable model and (b) the residual ordination based on the inclusion of measured predictors, with pond colour codes representing their elevation values (included variables detailed in panel (e)). Panel (c) shows the covariation estimates among frog species abundance due to similar response to measured predictors, and panel (d) shows the respective residual correlations after controlling for effects of predictors estimated by the joint species distribution model. Correlations range from negative (red), to neutral (white), to positive (blue), and are based on 95% high posterior density intervals that exclude zeros. Codes represent species abbreviations whose full names are given in Appendix S4.2. Panel (e) shows the relative proportions of variance attributed to mean annual temperature (MAT), net primary productivity (NPP), percentage of natural vegetation within elevational bands (BHA), percentage of natural vegetation at pond surrounds (PHA), pond vegetation structure (PVS), vegetation type (VEG), total area within elevational bands (Area), water surface cover (WSC), pond surface area (PSA),

and to the latent variables (LV) in frog species abundance. Bars show species-specific responses (species ordered by the highest proportion attributed to mean annual temperature) where legend indicates species averages. See Appendix S8.6 for specific values of each predictor for each species.

2.5 DISCUSSION

To the best of our knowledge, this is the first comprehensive study documenting transitions in anuran diversity along a steep elevation gradient (range of 1,500 m) of the Brazilian Atlantic Forest that simultaneously tests multiple hypotheses explaining these patterns. In this study, frog species richness showed a hump-shaped distribution while frog abundance was high in the lowlands but decreased at mid- to high elevations. The variation in frog species richness was best explained by the available area of natural habitats within elevational bands, whereas changes in mean annual temperature best explained frog abundance along the elevational gradient. In addition, we observed marked compositional divergence between frog assemblages from lowland to mid-to-high-elevation sites, which was also best explained by changes in temperature.

The mid-elevational peak in species richness we found here is consistent with previous studies on vertebrate elevational ranges, for which this pattern is considered to be the most pervasive (e.g. Gebert et al., 2019; McCain, 2010; McCain & Grytnes, 2010). In terms of anurans, most elevational gradients worldwide show a curvilinear relationship between species richness and elevation for these ectotherm vertebrates (McCain & Sanders, 2010). However, subtropical mountain ranges have been poorly sampled, and our study provides new support for the mid-elevational richness peak, suggesting that this can also be a more universal pattern for frogs. In addition, our results are at odds with the only other anuran study conducted along an AF elevational gradient (Ilha Grande island tropical coastal forests; narrower range of 750 m), which found a richness peak at low elevations (Goyannes-Araújo et al., 2015). These results reinforce that emergent patterns may vary within a single taxonomic group (McCain & Grytnes, 2010) and highlight the need for more rigorous surveys to be carried out along other tropical and subtropical elevational gradients.

Yet, there is still no consensus on the operational mechanisms promoting this pattern, which appears to be driven by a complex interplay of different predictors (Beck et al., 2017; Lomolino, 2001). We evaluated the support for most frequently proposed hypotheses explaining elevational patterns of species richness (e.g. Laiolo et al., 2018; McCain et al., 2018; Wu et al., 2013). Surprisingly, frog species richness was positively related to only landscape-scale habitat amount. This indicates that ponds located in areas containing more native vegetation should also harbour more frog species. This provides direct support for the habitat amount hypothesis (HAH; Fahrig, 2013), rather than the more general species-area relationship. The HAH was also found to be important in predicting taxonomic diversity in small mammals and functional diversity in frogs in highly fragmented Atlantic Forest landscapes (Almeida-Gomes et al., 2019; Vieira et al., 2018).

Areas corresponding to more extensive natural vegetation are more likely to harbour a higher diversity of suitable (micro)habitats and thereby confer a higher chance of accommodating habitat specialist species (Henneron et al., 2019; Leibold et al., 2004). Many frog species are considered habitat specialists and their local occupancy depends exclusively on some environmental conditions. For instance, *Ischnocnema henselii* exhibits direct development and depends on moist leaf-litter to lay their eggs (Haddad & Prado, 2005). Similarly, *Fritziana mitus* is found in epiphytic bromeliads, which they use for shelter, foraging, ovipositing and raising their tadpoles (Walker et al., 2018). At SJNP, these two species were only found where their specific microhabitat requirements were present. This highlights the strict dependence of some species on specific microhabitat types, which can partly explain the mid-elevational species richness peak documented here. At the elevational band scale, overall natural vegetation cover ranged from 57% to 99% (mean = 70±12%, SD; Appendix S1.1) and was positively correlated with elevation ($r = 0.81$, $p < .001$). This positive effect therefore indicates sufficiently strong environmental filtering in excluding species from unsuitable habitat areas along the elevation gradient. Like most topographically dissected landmasses worldwide, lowland Atlantic Forest areas succumbed to the heaviest impacts of agricultural land use, particularly compared to adjacent high-elevation forest lands (Tabarelli et al., 2010), and this reflects the strong positive relationship uncovered here between elevation and primary habitat amount. Moreover, we cannot rule out the possibility that lowland areas in the past retained higher anuran species diversity. For instance, water body density (e.g. ponds) throughout the entire 785,400-hectare planimetric area of our study region decreases at increasingly higher elevations (see Appendix S9.3). Water body density can also be seen as proxy of suitable habitat conditions for anurans, given that many species use them to reproduce (Crump, 2015; Haddad et al., 2013). We would therefore expect that higher lowland density of water bodies could also lead to higher species packing. Wachlevski et al. (2014) recorded twice as many frog species (n = 32) within similar lowland ranges (240 m - 490 masl) at Serra do Tabuleiro State Park, a protected area ~75 km east of our study landscape. Serra do Tabuleiro is one of the largest AF remnants in southern Brazil and most of its lowlands still remain relatively intact (MMA, 2000). In this context, historical land use trajectories—that are stacked against the integrity of contemporary lowland habitats—likely contribute to the observed pattern of frog species richness.

Habitat patch area is widely considered a major determinant of vertebrate species richness (Belmaker & Jetz, 2015; Rosenzweig, 1995). In general, larger areas tend to harbour more individuals, thereby reducing local extinction rates, and promote higher levels of habitat diversity and heterogeneity (Rosenzweig, 1995). However, habitat area per se (i.e. pond size and area of elevational bands) was a poor predictor of frog species richness, which is consistent with montane regions in China (Fu et al., 2006; Hu et al., 2011; see also Bueno et al. (2019) for a recent discussion on island species-area relationships). We found no support for the habitat complexity hypothesis even by taking into account many distinct montane habitats spanning a broad spectrum of habitat complexity (Figure 4; Table S1.1). Although local habitat complexity was not an important predictor of frog diversity, previous studies have found that higher local habitat complexity promotes species diversity, which is attributed to greater numbers of suitable sites for anuran egg-laying, vocal activity and shelter against predators (e.g. Vasconcelos et al., 2014). Species inhabiting low-complexity habitats may exhibit temporal segregation in pond use (Vasconcelos & Rossa-Feres, 2005), and this resource partitioning could partly explain the co-occurrence of similar frog diversity compared to more complex habitats. In summary, local habitat complexity seems to be species and/or system dependent and is not an essential element for pond-dwelling frog diversity along the elevational gradient.

Our data also indicate that neither temperature nor a proxy of habitat productivity was important predictors of frog species richness. This implies that, although anurans exhibit a critical thermal minimum lower than other ectothermic vertebrates (Buckley et al., 2012), their physiological limitations do not necessarily restrict their distribution along the elevational gradient. Indeed, some subtropical Brazilian frog species are known to be reproductively active all year-round, even showing physiological and behavioural adaptations to exploit cold environments (Kiss et al., 2008; Rossa-Feres & Jim, 1994). Should these limitations hold true, we would expect a monotonic upslope decline in frog species richness, which does not reflect our data. Productivity was high at low elevations but was not followed by a monotonic upslope decline, even though ~40% of the variance in productivity was explained by ambient temperature. This suggests that available potential energy may not be limiting along the elevation gradient, which could lead to similar levels of food availability for frogs. In addition, freshwater pond environments are likely to buffer upslope declines in local productivity and none of the ponds we surveyed ever freeze even during severe winters, even though widespread frosts are common above 800 masl. We acknowledge that we did not quantify food resource availability directly. However, both arthropod species richness and abundance, which comprise the bulk of anuran diets (Carvalho-Rocha et al., 2018; Solé & Rödder, 2010), are positively related to productivity (Schuldt et al., 2019), which may support this hypothesis. Frog species richness was apparently decoupled from frog abundance and productivity, lending little if any support to the "more-individuals-hypothesis" in our study system, although further studies on food availability along elevational gradients are needed.

Frog abundance was also decoupled from productivity but was positively affected by temperature. Lower temperatures may impose prohibitive limitations on anuran reproductive success, even in cold-adapted species (Kiss et al., 2008; Navas et al., 2013), which may result in small populations at high-elevation sites. For instance, lower temperatures can impose changes in species phenology and restrict breeding seasons to shorter periods, but can also increase the time to complete larval metamorphosis and affect tadpole survival (Amat & Meiri, 2017; Bernal & Lynch, 2013). While these mechanisms can explain the lower frog abundance at lower temperatures, we highlight that more physiological and behavioural studies are needed to help us better understand the mechanisms behind these patterns.

The latent variable model showed that lowland frog assemblages were very distinct compared to those in the highlands. Differentiation among frog assemblages along the elevational gradient was also observed in palaeotropical montane areas in Tanzania (Zancolli et al., 2014), China (Hu et al., 2011) and Borneo (Menegon & Salvidio, 2005). This observed segregation is consistent with variation in vegetation macromosaics across our study region. This suggests that each vegetation formation retains its own pool of species adapted to local environmental conditions and exploiting specific microhabitats (Crump, 2015; Haddad & Prado, 2005). Thus, it is likely that environmental filters may operate in promoting differentiation among frog assemblages, mirroring what we found for species richness.

Our results confirm that local abiotic conditions, mainly temperature, play an important role in predicting frog assembly composition. For example, *Scinax tymbamirim*, *Leptodactylus gracilis* and *Rhinella abei* were common sympatric species at warmer sites (lower altitudes; Figure 2) and were strongly positively correlated with one another and this climatic predictor. These species were also negatively correlated with species that are also typically sympatric at cold, high-elevation sites, such as *Boana leptolineata*, *S. granulatus* and *Physalaemus gracilis* (Figure 2). We detected just a few positive relationships between frog species that could be associated with positive interactions. Competition among frog species, specially noncongeners, is often acknowledged to be rare (Cloyed & Eason, 2017; Duellman, 1999), and general assembly process is more related to responses to environmental conditions (e.g. Ernst & Rödel, 2006; Indermaur et al., 2010), corresponding to a Gleasonian community worldview (Gleason, 1926). This strongly suggests that frog assemblages along the SJNP elevational gradient are formed by species with similar thresholds of thermal tolerance.

Although frog species richness and assemblages were associated with their own key predictors, both were conditional on effects of environmental filtering, providing further evidence that this process is the main driver of different levels of frog diversity (Werner et al., 2007). Several studies have shown that climatic gradients are important drivers of the spatial distribution of neotropical anurans at large biogeographic scales (Luiz et al., 2016; Silva et al., 2014; Vasconcelos et al., 2014). However, we have shown that steep climatic variation imposed by elevational settings is also important in shaping frog assemblages, even at a relatively narrow spatial scale.

2.6 CONCLUSIONS

Patterns of heterotherm diversity along tropical elevational gradients remain poorly explored. Our study shows that different components of anuran species diversity are influenced by mechanisms related to environmental filtering along the elevational gradient. Specifically, frog species richness was strongly associated with the proportion of natural habitats remaining within each elevational zone, while frog abundance was highly associated with mean annual temperature. This reinforces the detrimental effects of the widespread historical degradation of lowland areas in the Atlantic Forest, which is directly associated with the leading cause of declines in frog diversity worldwide. Climatic conditions were strong determinants of frog assemblage structure along the elevational gradient. Lowland assemblages clearly diverge from those at mid- to high elevations, leading to two distinct groups of frog species. Nonetheless, future studies considering species functional traits and phylogenetic relationships may help elucidate if climatic restrictions are due to niche conservatism or species-specific environmental filtering operating on life history characteristics. Lastly, the entire elevational gradient we studied was clearly important in retaining the overall regional scale (gamma) diversity. This indicates that anthropogenic habitat disturbance has exerted an enormous overarching influence on montane frog diversity, reinforcing the need for effectively protected areas that are well distributed across all elevational zones.

2.7 AKNOWLEDGEMENTS

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2.8 DATA AVAILABILITY STATEMENT

The raw data are provided in Appendix S1.1 and S5.3.

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2.10 SUPPLEMENTARY INFORMATION

Supplementary Information for

HABITAT AMOUNT AND AMBIENT TEMPERATURE DICTATE PATTERNS OF ANURAN DIVERSITY ALONG A SUBTROPICAL ELEVATIONAL GRADIENT

Vítor Carvalho-Rocha, Carlos A. Peres, Selvino Neckel-Oliveira

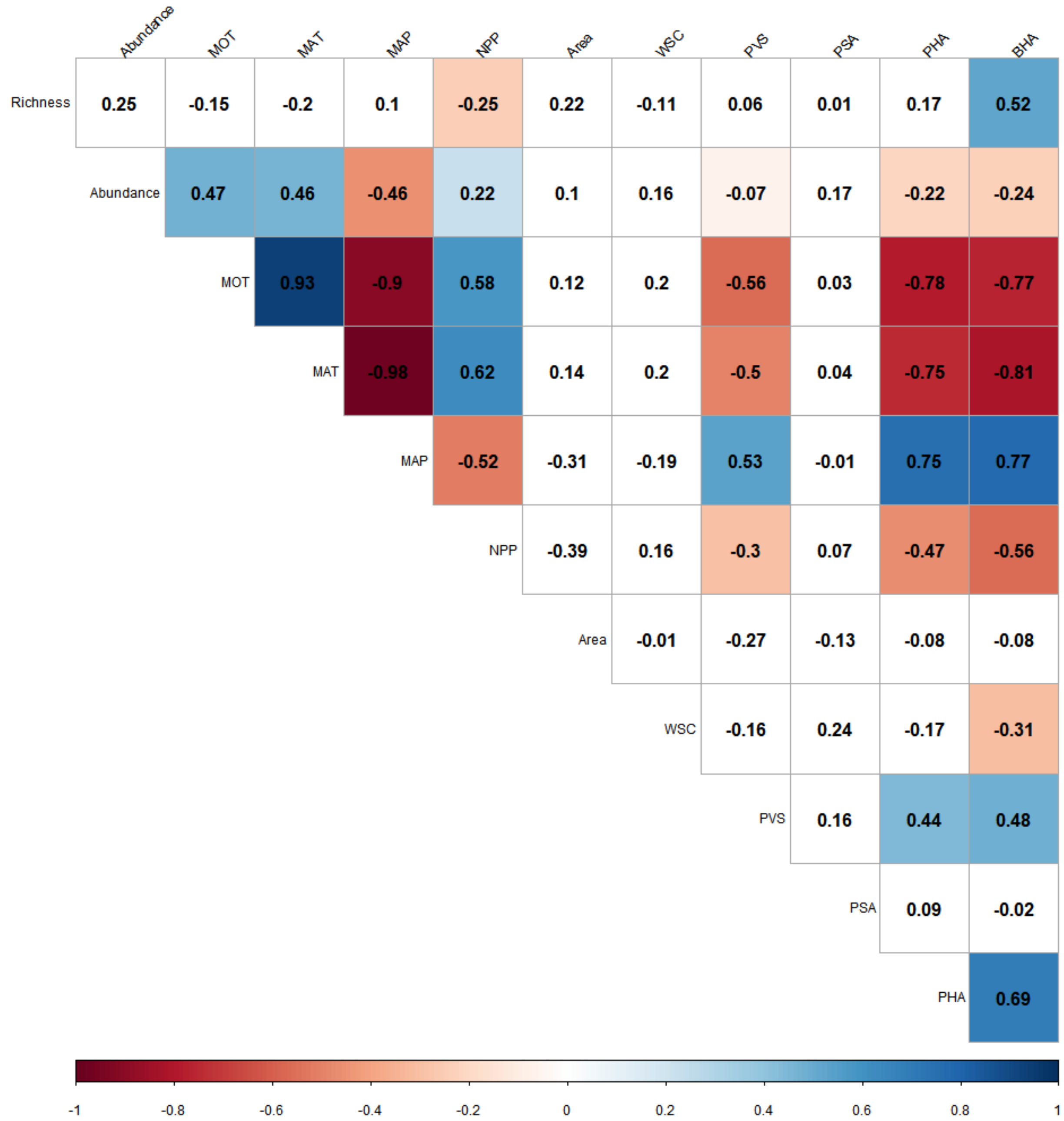
Appendix S1

Detailed description of perennial ponds surveyed in this study, with their respective measured predictors.

TABLE S1.1 Code names, geographic position, elevation and respective values of measured predictors of each 38 surveyed ponds at the São Joaquim National Park and surrounds, Santa Catarina, Brazil. MOT: mean observed temperature during surveys; MAT: mean annual temperature; MAP: mean annual accumulated precipitation; NPP: net primary productivity; WSC: water surface cover; PVS: pond vegetation surface; PSA: pond surface area; PHA: pond habitat amount; BAH: band habitat amount; VEG: vegetation type (edf: evergreen dense forest; maf: mixed Araucaria forest).

Pond	**Longitude**	**Latitude**	**Elevation**	**MOT**	**MAT**	**MAP**	**NPP**	**Area**	**WSC**	**PVS**	**PSA**	**PHA**	**BHA**	**VEG**
F104	-49.475843	-28.27096	312	16.63	18.5	1474.56	1671.03	724.59	0.36	0	1014.43	0.56	0.57	edf
F105	-49.471251	-28.266882	322	15.72	18.45	1476.86	1678.95	713.28	0.39	0.23	6691.03	0.64	0.57	edf
F102	-49.448269	-28.22512	328	17.05	18.43	1477.95	1685.93	709.57	0.74	0	1886.05	0.28	0.57	edf
F101	-49.458121	-28.21171	352	15.68	18.11	1499.97	1706.2	677.48	0.12	0.07	688.18	0.26	0.57	edf
F103	-49.470778	-28.213213	384	16.47	18.19	1494.25	1692.63	603.68	0.44	0	553.89	0.14	0.63	edf
F205	-49.45317	-28.177236	442	16.59	17.92	1509.63	1715.53	447.07	0.49	0.53	947.28	0.08	0.68	edf
F201	-49.477235	-28.282905	465	15.62	17.81	1516.86	1725.65	389.12	0	0.78	1226.36	0.48	0.72	edf
F204	-49.485467	-28.213576	475	15.7	17.73	1520.03	1724.83	366.97	1	0	1854.6	0.3	0.62	edf
F203	-49.487366	-28.261007	477	16.69	17.72	1520.43	1728.89	361.48	0.32	0.22	845.52	0.74	0.63	edf
F202	-49.363367	-28.130717	571	15.43	17.17	1554.38	1732.73	254.4	0	0.64	5300.75	0.37	0.82	edf
F303	-49.454128	-28.160606	601	15.68	17.04	1563.83	1731.9	239.8	0.79	0.52	2249.38	0.66	0.75	edf
F304	-49.473162	-28.164016	621	14.95	16.95	1569.29	1733.89	253.23	0.44	0.44	6722.97	0.58	0.84	edf
F305	-49.479192	-28.170122	639	15.04	16.91	1572.19	1733.27	203.56	0.67	0	911.65	0.57	0.73	edf
F302	-49.404297	-28.126418	708	16.15	16.51	1590.97	1725.73	248.06	0.18	0	3276.79	0.63	0.81	edf
F301	-49.380148	-28.123942	712	14.83	16.5	1591.24	1721.49	248.87	0.17	1	835.98	0.7	0.8	edf
F402	-49.476978	-28.043779	929	14.59	15.43	1598.04	1637.96	611.81	0.64	0.16	1202.78	0.21	0.62	maf
F403	-49.443083	-28.051046	958	14.72	15.28	1606.61	1692.3	492.86	0.15	0.33	209.32	0.31	0.7	maf
F405	-49.416454	-28.075432	983	15.04	15.14	1614.51	1702.6	443.59	0.05	0	2381.7	0.47	0.79	maf
F404	-49.42869	-28.067771	985	14.57	15.13	1614.57	1703.18	440.98	0.18	0.19	538.16	0.49	0.79	maf
F401	-49.485991	-28.069147	991	14.05	15.1	1615.85	1716.67	433.87	0.33	0	222.6	0.85	0.78	maf
F501	-49.468315	-28.043531	1024	13.24	14.96	1616.48	1701.11	413.38	0.04	0.53	1551.63	0.34	0.83	maf
F502	-49.463754	-28.054644	1131	13.08	14.49	1619.02	1572.78	505.35	0.68	0.35	718.91	0.52	0.91	maf
F504	-49.550437	-28.081191	1139	10.81	14.46	1619.64	1564.71	520.26	0.03	0.74	4325.45	0.95	0.91	maf
F505	-49.658752	-28.329245	1198	11.73	14.22	1626.08	1483.73	684.4	0	0	780.89	0.77	0.91	maf
F601	-49.564759	-28.292319	1303	12.38	13.74	1656.06	1456.57	863.05	0.89	0	675.89	0.86	0.91	maf
F602	-49.557812	-28.281763	1330	13.32	13.61	1666.02	1451.02	863.68	0.11	0.48	5989.96	0.88	0.91	maf
F605	-49.435689	-28.093822	1337	13.18	13.58	1668.66	1458.5	861.08	0.42	1	524.94	0.87	0.91	maf
F604	-49.63574	-28.142349	1353	10.15	13.51	1674.48	1466.62	837.09	0.02	0.92	595.23	0.98	0.91	maf
F603	-49.560454	-28.314437	1373	12.71	13.41	1682.6	1469.85	818.24	0.13	0	422.23	0.94	0.91	maf
F704	-49.534131	-28.083537	1425	9.96	13.15	1699.05	1526.44	644.92	0	0.66	720.88	0.96	0.9	maf
F705	-49.541867	-28.089954	1444	11.42	13.33	1688	1675.42	581.74	0.19	1	735.18	0.9	0.93	maf
F703	-49.490391	-28.11551	1546	11.84	12.78	1728.25	1238	298.56	0.06	1	356.93	0.63	0.89	maf
F702	-49.633818	-28.156881	1575	9.35	12.45	1756.62	1638.13	246.69	1	1	552.05	0.98	0.86	maf
F701	-49.593613	-28.168796	1586	11.48	12.38	1759.85	1631.58	226.36	0.02	0.52	351.53	0.97	0.85	maf
F803	-49.603651	-28.165981	1627	10.6	12.3	1762	1587.6	155.04	0	0.57	475.68	0.97	0.83	maf
F804	-49.518134	-28.097339	1633	10.75	12.17	1774.92	1592.45	148.55	1	1	13547.38	0.99	0.81	maf
F802	-49.508118	-28.09821	1636	10.67	12.17	1774.85	1597.27	142	0.06	0.88	415.93	0.96	0.82	maf
F801	-49.480814	-28.127386	1796	9.82	11.75	1817	1650.68	3.2	0	0.53	522.08	0.99	0.99	maf

Appendix S2



	Abundance	MOT	MAT	MAP	NPP	Area	WSC	PVS	PSA	PHA	BHA
Richness	0.25	-0.15	-0.2	0.1	-0.25	0.22	-0.11	0.06	0.01	0.17	0.52
Abundance		0.47	0.46	-0.46	0.22	0.1	0.16	-0.07	0.17	-0.22	-0.24
MOT			0.93	-0.9	0.58	0.12	0.2	-0.56	0.03	-0.78	-0.77
MAT				-0.98	0.62	0.14	0.2	-0.5	0.04	-0.75	-0.81
MAP					-0.52	-0.31	-0.19	0.53	-0.01	0.75	0.77
NPP						-0.39	0.16	-0.3	0.07	-0.47	-0.56
Area							-0.01	-0.27	-0.13	-0.08	-0.08
WSC								-0.16	0.24	-0.17	-0.31
PVS									0.16	0.44	0.48
PSA										0.09	-0.02
PHA											0.69

FIGURE S2.1 Pearson correlations values between measured predictors and frog species richness and abundance among ponds distributed along the entire SJNP elevational gradient and surrounding areas, state of Santa Catarina, Brazil. MOT: mean observed temperature during surveys; MAT: mean annual temperature; MAP: mean annual accumulated precipitation; NPP: net primary productivity; WSC: water surface cover; PVS: pond vegetation surface; PSA: pond surface area; PHA: pond habitat amount; BAH: band habitat amount. Blue and red boxes respectively indicate positive and negative significant correlations ($p < 0.05$).

Appendix S3

Spatial autocorrelation

The presence of any residual spatial autocorrelation on both species richness and abundance was tested following the protocol proposed by Bauman, Drouet, Fortin & Dray (2018) using the R package ‘adespatial’ (Dray et al., 2017). We used Moran’s eigenvector maps (MEM) based on 42 different spatial weighting matrices (SWM) to represent the possible spatial structure present in our dataset in different ways (Bauman et al., 2018). The construction of multiple SWM is advised given that the selection of MEM depends directly on the type of SWM (Bauman, Drouet, Dray & Vleminckx, 2018). We constructed the SWM combining: (i) five connectivity matrices (i.e., Delaunay triangulation, Gabriel’s graph, relative neighborhood graph, minimum spanning tree, distance-based matrix connecting all site at a distance equals to the largest edge of the minimum spanning tree); (ii) four weight matrices (i.e., without weight between connections (binary), linear, concave-down and concave-up weighting functions); and (iii) two connective styles (i.e., binary and row standardized), in addition to two Principal Coordinates of Neighbourhood Matrices (PCNM) in both connective styles. For specific details of matrix calculations, see the ‘adespatial’ R package guidelines (Dray et al., 2017).

The MEM selection was performed using the optimized approach “MIR” that minimizes residual autocorrelation and keeps the maintenance of a high explanatory power for environmental predictors by selecting as few MEMs as possible (Bauman, Drouet, Dray, et al., 2018). For each SWM, this selection procedure tests the significance of the Moran’s I in the vector of interest (in our case the residuals of the species richness and abundance models). It then searches for the MEM variable best minimizing the value of the Moran’s I, creates a model of Y against this MEM variable, and tests the significance of the Moran’s I of this new model residuals. The procedure goes on until the Moran’s I of the model residuals is no longer significant. Following this procedure, not a single MEM was selected (Table S3.2), indicating a lack of spatial autocorrelation in our data and confirming the reliability of our results.

References

Bauman, D., Drouet, T., Dray, S., & Vleminckx, J. (2018). Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. Ecography, 41, 1638-1649.

Bauman, D., Drouet, T., Fortin, M. J., & Dray, S. (2018). Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. Ecology, 99, 2159-2166.

Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Legendre, P., & Wagner, H. H. (2017). Adespatial: multivariate multiscale spatial analysis. R package 0.3-8.

TABLE S3.2 Significance of Moran's I spatial autocorrelation based on 42 different weighting matrices on models predicting frog abundance and species richness across the 38 surveyed ponds along the elevational gradient at the São Joaquim National Park and surrounds, Santa Catarina, Brazil. DBM: distance-based matrix equals to the largest edge of the minimum spanning tree; Del: Delaunay triangulation; Gab: Gabriel's graph; MST: minimum spanning tree; RNG: relative neighbourhood graph; PCNM: principal coordinates of neighbourhood matrices; Bin: binary weight; Cdw: concave-down weight; Cup: concave-up weight; Lin: linear weight; B: Binary connective styles; W: row standardized connective styles.

	Abundance		Richness	
Spatial weight matrix	Morran's I	*p*-value	Morran's I	*p*-value
PCNM_B	0.04172046	0.8890389	-0.02488738	0.9999873
Del_Bin_B	0.06868417	0.9575724	-0.15036269	1
Del_Lin_B	0.03365229	0.9979449	-0.15614629	1
Del_Cdw_B	0.04735974	0.9927271	-0.15393276	1
Del_Cup_B	0.05075142	0.9908969	-0.13926118	1
Gab_Bin_B	0.10952092	0.9623683	-0.17848736	1
Gab_Lin_B	0.08966733	0.9876814	-0.17165968	1
Gab_Cdw_B	0.07774752	0.9930669	-0.18064812	1
Gab_Cup_B	0.10714751	0.9806159	-0.14030084	1
RNG_Bin_B	0.10917554	0.9873257	-0.12724977	1
RNG_Lin_B	0.14729274	0.9477164	-0.08685149	1
RNG_Cdw_B	0.13478746	0.9611488	-0.13153002	1
RNG_Cup_B	0.12952399	0.9746867	-0.07866852	1
MST_Bin_B	0.16029819	0.9223878	-0.11092817	1
MST_Lin_B	0.183192	0.9099271	-0.07729263	1
MST_Cdw_B	0.18962653	0.8759347	-0.11653011	1
MST_Cup_B	0.16142795	0.9372245	-0.06739684	1
DBM_Bin_B	0.04155556	0.8715461	-0.02355176	0.9999871
DBM_Lin_B	0.04241746	0.9623683	-0.06336396	1
DBM_Cdw_B	0.05522732	0.8195398	-0.05101323	1
DBM_Cup_B	0.04287269	0.9136693	-0.03808673	0.9999999
PCNM_W	0.06684623	0.8433879	-0.02717285	0.9999969
Del_Bin_W	0.07260744	0.9643493	-0.15817261	1
Del_Lin_W	0.05797616	0.9901262	-0.14743443	1
Del_Cdw_W	0.06309348	0.980018	-0.15591643	1
Del_Cup_W	0.07147462	0.9780062	-0.13067176	1
Gab_Bin_W	0.11238203	0.9720987	-0.12637513	1
Gab_Lin_W	0.10618993	0.9823992	-0.11420684	1
Gab_Cdw_W	0.09388498	0.98878	-0.12357482	1
Gab_Cup_W	0.12072141	0.9631005	-0.10260721	1
RNG_Bin_W	0.11477412	0.986128	-0.06088704	1
RNG_Lin_W	0.16420483	0.9363159	-0.04401655	0.9999999
RNG_Cdw_W	0.14799792	0.9546866	-0.06346327	1
RNG_Cup_W	0.13940465	0.9668093	-0.03312699	0.9999998
MST_Bin_W	0.17899735	0.8918505	-0.06590236	1
MST_Lin_W	0.21036268	0.8223962	-0.04316223	0.9999999
MST_Cdw_W	0.2121707	0.8203604	-0.06823899	1

MST_Cup_W	0.18294155	0.9051434	-0.02815956	0.9999995
DBM_Bin_W	0.06551132	0.8739047	-0.02638852	0.9999948
DBM_Lin_W	0.09354933	0.8349144	-0.05199271	1
DBM_Cdw_W	0.09674097	0.7122994	-0.04877903	1
DBM_Cup_W	0.08242515	0.815803	-0.03338239	0.9999991

Appendix S4

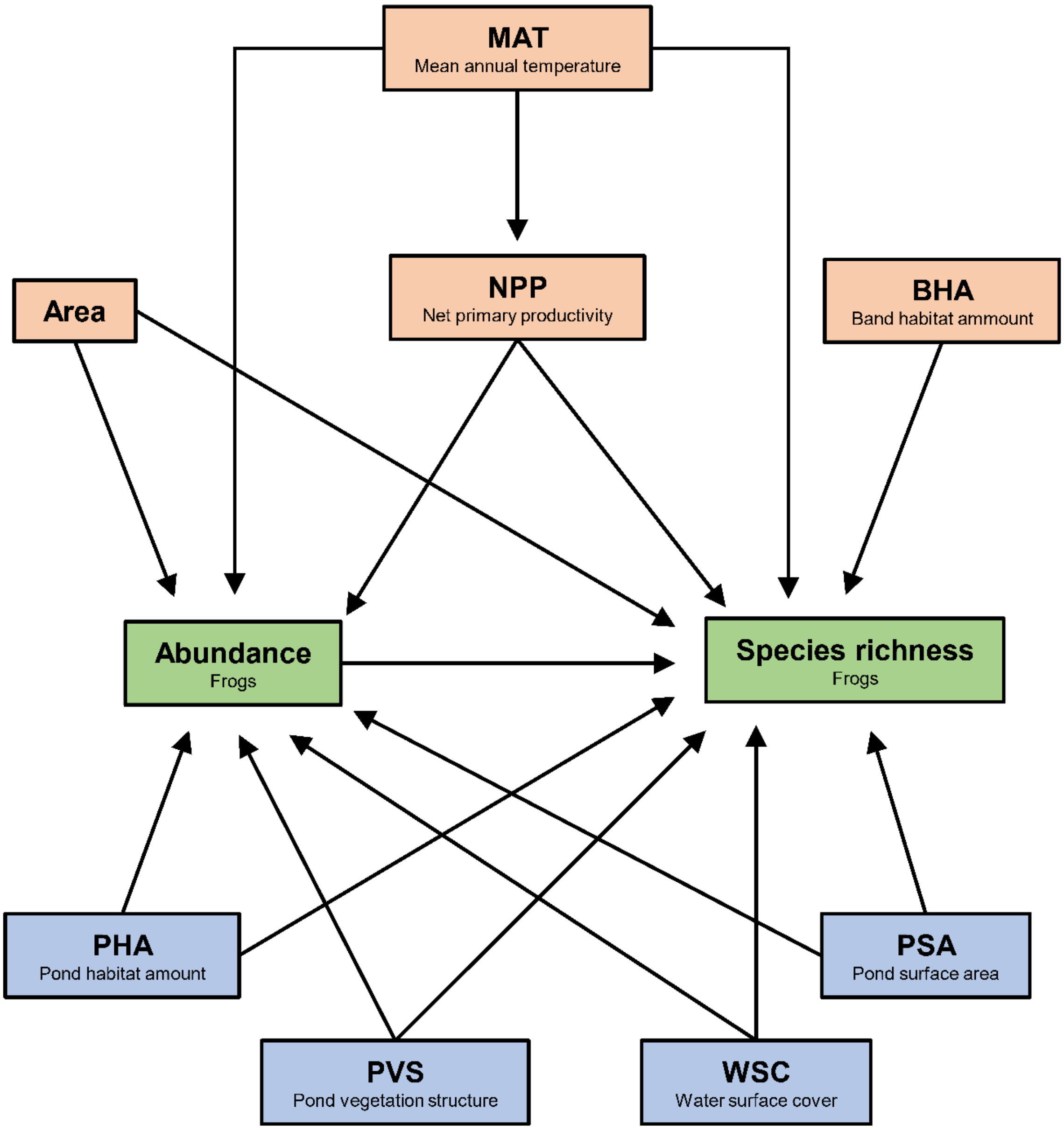


FIGURE S4.2. Theoretical causal diagram for the proposed mechanisms of frog species richness and abundance variation across the 38 surveyed perennial ponds along the elevational gradient at the São Joaquim National Park and surrounding areas, Santa Catarina, Brazil. All relationships were hypothesized to be positive.

Appendix S5

TABLE S5.3 Frog species, name abbreviations, and their total abundance within the 38 surveyed ponds along the SJNP elevational gradient, Santa Catarina, Brazil. Ponds are ordered by elevation and follow code provided at Table S1.1.

Species	**Abbreviation**	**Ponds**																																			
		F104	F105	F102	F101	F103	F205	F201	F204	F203	F202	F303	F304	F305	F302	F301	F402	F403	F405	F404	F401	F501	F502	F504	F505	F601	F602	F605	F604	F603	F704	F705	F703	F702	F701	F803	F804	F802	F801
Adenomera araucaria	Ade.ara	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Aplastodiscus perviridis	Apl.per	0	0	0	0	0	0	0	0	0	0	0	0	0	0	36	2	0	2	9	4	0	28	5	0	1	0	0	4	8	2	0	0	11	7	0	1	0	0
Boana bischoffi	Boa.bis	89	243	97	90	53	58	3	127	81	132	340	296	149	67	5	108	109	108	40	19	141	141	162	0	0	0	236	1	0	2	44	49	0	0	0	0	32	0
Boana faber	Boa.fab	47	51	20	13	3	38	12	11	28	4	20	56	96	32	0	10	0	6	3	3	37	16	0	4	0	0	42	0	0	0	0	0	0	0	0	0	0	0
Boana joaquini	Boa.joa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	28	0	0	0	0	0	0	5	0	1	0	1	36	128	0	0	0	0	0	0
Boana leptolineata	Boa.lep	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	5	0	0	31	3	1	17	14	13	26	5	27	17	24	0	0	0	67	5
Boana marginata	Boa.mar	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boana prasina	Boa.pra	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	2	0	0	0	0	0	8	23	0	8	0	9	2	16	15	1	0	0	2	0	47	0
Dendropsophus microps	Den.mic	0	4	7	0	0	0	0	72	0	0	14	4	0	0	189	4	0	0	0	0	0	33	0	0	0	0	25	0	0	0	4	0	0	0	0	0	0	0
Dendropsophus minutus	Den.min	0	0	0	0	0	0	0	0	0	0	0	27	30	16	0	121	172	19	12	114	35	164	66	54	50	22	197	171	63	63	78	43	1	17	32	2	104	1
Dendropsophus nahdereri	Den.nah	0	4	0	0	0	0	0	11	0	0	2	6	18	14	0	0	0	4	0	7	1	0	8	0	0	0	130	2	0	2	47	6	0	2	0	0	5	8
Elachistocleis bicolor	Ela.bic	0	1	0	0	2	0	2	2	0	0	0	10	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fritziana mitus	Fri.mit	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hylodes meridionalis	Hyl.mer	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ischnocnema henselii	Isc.hen	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ischnocnema aff. *manezinho*	Isc.man	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Leptodactylus gracilis	Lep.gra	4	25	44	17	38	11	16	35	6	0	29	31	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptodactylus latrans	Lep.lat	80	168	62	28	36	118	123	11	214	27	33	144	58	35	5	15	37	50	6	11	2	27	4	0	4	23	17	0	4	3	0	4	0	0	0	0	7	1
Leptodactylus plaumanni	Lep.pla	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	1	7	16	9	5	2	15	9	5	1	11	0	2	9	5	6	0	0	0	0	19	0	6
Ololygon argyreornata	Olo.arg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ololygon catharinae	Olo.cat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	1	0	0	0	0	0	0
Ololygon berthae	Sci.ber	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	0	0	31	0	0	0	0	0	0	28	21	3	0	0	2	9	7	0
Ololygon rizibilis	Sci.riz	0	0	0	0	0	0	0	2	0	0	0	0	0	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllomedusa distincta	Phyl.dis	0	0	0	0	0	0	0	0	0	0	1	0	96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physalaemus lateristriga	Phy.lat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physalaemus cuvieri	Phy.cuv	6	15	2	3	5	22	0	18	19	0	19	27	8	13	0	11	7	1	12	7	4	8	0	11	8	0	0	0	4	1	0	0	0	0	0	0	0	0
Physalaemus gracilis	Phy.gra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42	23	1	22	11	3	26	45	5	2	16	0	0	8	0	11	0	0	10	0	8	1	14
Physalaemus nanus	Phy.nan	0	13	46	4	0	0	47	0	0	0	38	21	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0	0
Pseudis cardosoi	Pse.car	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	6	44	52	0	63	17	0	0	0	0	0	0	0	0	0
Proceratophrys boiei	Pro.boi	0	0	0	0	0	0	0	0	0	6	1	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhinella abei	Rhi.abe	0	1	1	0	1	1	4	0	4	9	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhinella henseli	Rhi.hen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhinella icterica	Rhi.ict	1	0	8	2	12	9	7	0	5	56	0	18	0	193	0	4	8	36	79	2	18	10	3	0	2	24	0	0	3	1	2	0	0	7	1	1	13	3
Scinax fuscovarius	Sci.fus	0	0	0	0	0	0	4	0	0	1	1	0	4	114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scinax granulatus	Sci.gra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31	0	0	1	5	0	33	0	13	13	3	14	2	0	0	8	16	21	38
Scinax perereca	Sci.per	3	2	12	0	3	10	0	66	7	0	29	82	122	143	13	9	12	6	18	38	74	0	21	0	4	0	145	0	0	4	9	1	0	0	0	0	0	0
Scinax squalirostris	Sci.squ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	17	0	22	0	0	0	0	0	0	0	0	9	0	0	3
Scinax tymbamirim	Sci.tym	142	336	9	15	42	81	0	0	168	5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaenorhynchus surdus	Sph.sur	0	56	5	0	16	53	0	0	10	0	0	120	0	0	0	45	9	0	0	0	0	16	5	0	0	0	0	0	0	2	2	0	0	0	0	0	14	0
Trachycephalus dibernardoi	Tra.dib	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0

Appendix S6

TABLE S6.4 Frog species richness, Chao I estimated richness values and sample coverage across the 38 surveyed ponds along the SJNP elevational gradient, Santa Catarina, Brazil. Ponds were ordered from lowest to highest elevation and follow the codes provided in Table S1.1.

Pond	Observed Richness	Chao I	Sample Coverage (%)
F104	8	8	1
F105	13	14.998	0.998
F102	12	12.498	0.997
F101	8	8	1
F103	11	11.498	0.995
F205	10	10	1
F201	9	9	1
F204	10	11.249	0.997
F203	10	10	1
F202	11	11.996	0.992
F303	12	16.491	0.994
F304	19	19.499	0.999
F305	11	11	1
F302	10	10	1
F301	11	12.499	0.997
F402	12	12.499	0.997
F403	11	11.499	0.997
F405	14	16.241	0.988
F404	12	12	1
F401	15	15.498	0.996
F501	11	11.249	0.997
F502	12	12	1
F504	15	14	1
F505	11	11	1
F601	10	23.393	0.957
F602	11	11	1
F605	10	10	1
F604	10	10.996	0.993
F603	11	12	1
F704	17	17.894	0.98
F705	15	15.249	0.997
F703	11	15.483	0.989
F702	3	3	1
F701	5	5	1
F803	7	7.164	0.984
F804	8	9.964	0.965
F802	11	11	1
F801	9	9.987	0.975

Appendix S7

TABLE S7.5 Results of the Bayesian Structural Equation Modeling on estimated frog species richness and abundance along the SJNP elevational gradient, Santa Catarina, Brazil. The model was fit with local parameter estimates to account for the specific error distribution on each response variable. Table shows response variables included with their respective raw coefficient estimates, standard errors, lower and upper 95% credible intervals (Highest Posterior Density Interval), chain potential scale reduction factor (Rhat) and effective sample size (ESS). MAT: mean annual temperature; MAP: mean annual accumulated precipitation; NPP: net primary productivity; WSC: water surface cover; PVS: pond vegetation surface; PSA: pond surface area; PHA: pond habitat amount; BAH: band habitat amount.

Response	Predictor	Raw estimate	Standard error	Low 95% CI	Upper 95% CI	Rhat	ESS
Richness	Intercept	0.6499	1.3013	-1.9046	3.1354	1	1077
	MAT	0.011	0.0473	-0.0844	0.1053	1.01	1047
	NPP	0.0003	0.0005	-0.0007	0.0014	1	1094
	Area	0.0002	0.0002	-0.0002	0.0006	1	925
	BHA	1.9822	0.6358	0.6593	3.1872	1	1049
	PHA	-0.2169	0.2307	-0.6774	0.2364	1	1053
	WSC	0.0221	0.1363	-0.2358	0.3025	1	1064
	PVS	-0.0951	0.1254	-0.3354	0.1589	1	1083
	PSA	0	0	0	0	1	922
	Abundance	0.0003	0.0002	-0.0001	0.0007	1	1023
Abundance	Intercept	-0.1226	3.3073	-6.2871	6.5441	1	962
	MAT	0.3341	0.1081	0.1207	0.5511	1	941
	NPP	-0.0007	0.0016	-0.004	0.0022	1	876
	Area	0.0003	0.0006	-0.001	0.0014	1.01	811
	BHA	1.9993	1.51	-1.0551	4.964	1	1024
	PHA	-0.0647	0.5991	-1.2859	1.1178	1	915
	WSC	0.1196	0.4219	-0.7153	0.9939	1	929
	PVS	0.4974	0.3808	-0.3164	1.2515	1	981
	PSA	0	0.0001	-0.0001	0.0001		1064
NPP	Intercept	7.0914	0.0751	6.9425	7.2381	1	1050
	MAT	0.0199	0.0049	0.0103	0.0296	1	1035

Appendix S8

Table S8.6 Relative proportions of variance attributed to mean annual temperature (MAT), net primary productivity (NPP), elevational band habitat amount (BHA), pond habitat amount (PHA), pond vegetation structure (PVS), vegetation type (VEG), area within elevational bands (Area), water surface cover (WSC), pond surface area (PSA), and to the latent variables (LV) on the abundance of 28 frog species used in the joint species distribution model, along the SJNP elevational gradient, Santa Catarina, Brazil. Species are ordered as in Figure 5 of the main text.

Frog species	**MAT**	**NPP**	**BHA**	**PHA**	**PVS**	**VEG**	**Area**	**WSC**	**PSA**	**LV**
Leptodactylus gracilis	0.397363	0.203719	0.03183	0.028528	0.025367	0.06681	0.052496	0.050392	0.027065	0.116432
Boana faber	0.380658	0.047159	0.095735	0.04069	0.019833	0.025824	0.056268	0.012342	0.035866	0.285626
Leptodactylus latrans	0.354555	0.03905	0.043344	0.046244	0.032327	0.115456	0.039782	0.036986	0.019883	0.272372
Dendropsophus minutus	0.325553	0.033888	0.045762	0.029418	0.078047	0.03756	0.038383	0.012735	0.013953	0.3847
Boana bischoffi	0.311775	0.024921	0.027287	0.059408	0.032087	0.034698	0.022008	0.01379	0.01904	0.454987
Scinax tymbamirim	0.306727	0.112611	0.080817	0.029978	0.057391	0.062521	0.066777	0.060554	0.051695	0.17093
Rhinella abei	0.299856	0.130385	0.069078	0.036769	0.044542	0.040044	0.092215	0.088836	0.047484	0.150792
Physalaemus cuvieri	0.298035	0.067172	0.09048	0.026824	0.173654	0.058159	0.044959	0.034923	0.021969	0.183824
Scinax perereca	0.2359	0.049688	0.18441	0.023138	0.017731	0.034415	0.035019	0.029008	0.059688	0.331002
Elachistocleis bicolor	0.226509	0.088273	0.094692	0.077697	0.097325	0.03699	0.070601	0.048459	0.072068	0.187386
Physalaemus gracilis	0.224788	0.08663	0.050925	0.05129	0.083366	0.271063	0.036015	0.015878	0.050754	0.12929
Rhinella icterica	0.195672	0.132683	0.073604	0.127327	0.120093	0.051305	0.032932	0.08314	0.059323	0.123921
Dendropsophus microps	0.194893	0.070328	0.052449	0.047431	0.180197	0.017119	0.049885	0.168146	0.033953	0.185597
Scinax fuscovarius	0.174959	0.11512	0.09301	0.071381	0.059056	0.036984	0.141379	0.059677	0.065742	0.182691
Physalaemus nanus	0.16833	0.100126	0.075119	0.121077	0.122651	0.061978	0.083454	0.033911	0.075031	0.158324
Boana leptolineata	0.163203	0.031937	0.182114	0.164931	0.029079	0.078408	0.032985	0.031373	0.030267	0.255702
Ololygon berthae	0.163166	0.037066	0.087651	0.104318	0.068662	0.078988	0.05309	0.066896	0.038655	0.301508
Proceratophrys boiei	0.149273	0.125161	0.103937	0.070875	0.125513	0.03035	0.112897	0.049448	0.06099	0.171557
Scinax granulatus	0.147766	0.02088	0.065401	0.314162	0.050547	0.108108	0.02193	0.06833	0.036406	0.166471
Boana joaquini	0.129754	0.036169	0.120828	0.117561	0.047129	0.055067	0.071769	0.159056	0.051783	0.210885
Aplastodiscus perviridis	0.124923	0.154534	0.1341	0.05021	0.046503	0.078939	0.083926	0.055326	0.054899	0.216639

Boana prasina	0.124506	0.041922	0.096007	0.051301	0.032548	0.040035	0.039904	0.202838	0.055131	0.315808
Scinax squalirostris	0.109767	0.07097	0.088659	0.128431	0.135702	0.046204	0.050598	0.113512	0.060677	0.19548
Dendropsophus nahdereri	0.10215	0.040016	0.054452	0.097126	0.030048	0.061741	0.026684	0.028325	0.03119	0.528268
Sphaenorhynchus surdus	0.096681	0.094676	0.057677	0.074171	0.095704	0.044662	0.071484	0.061574	0.038703	0.364668
Rhinella henseli	0.091473	0.132043	0.087956	0.119765	0.072796	0.064082	0.070497	0.106381	0.082626	0.172381
Pseudis cardosoi	0.081224	0.172075	0.133902	0.057396	0.057234	0.048191	0.179113	0.051391	0.048304	0.17117
Leptodactylus plaumanni	0.074979	0.126255	0.240556	0.082954	0.028993	0.157841	0.05906	0.026168	0.087414	0.115781

Appendix S9

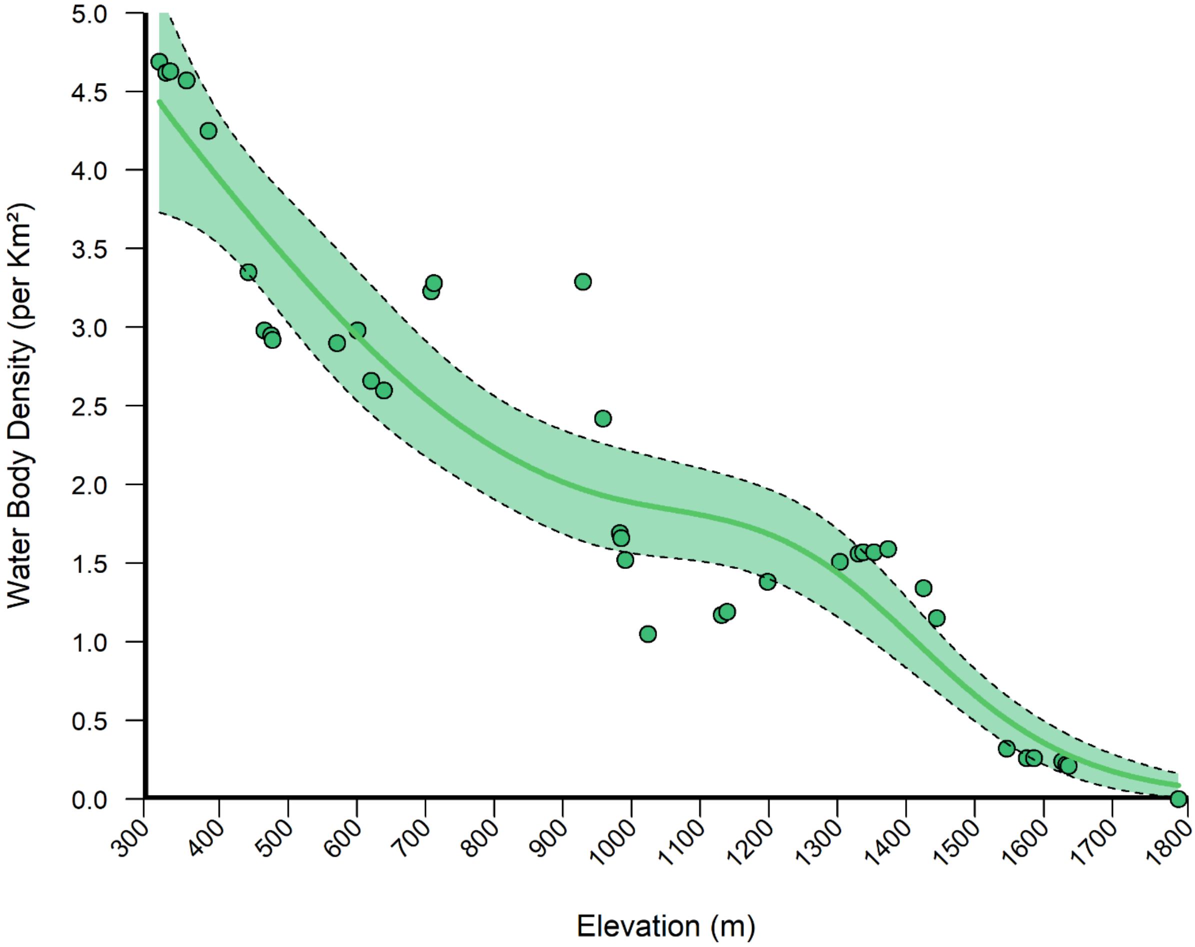


FIGURE S9.3 Variation in the landscape-wide density of water bodies within elevational bands along the SJNP elevational gradient and surrounding areas, Santa Catarina, Brazil. Green circles represent the number of water bodies per km² within each 100 m elevational band considering a range 50 m above and below the elevation of each pond. Solid lines represent main trend; dashed lines and green shading indicate the 95% credible interval computed using a Generalized Additive Model (GAM).

3 CAPÍTULO 2 - SEASONAL VARIATION IN PATTERNS OF ANURAN DIVERSITY ALONG A SUBTROPICAL ELEVATIONAL GRADIENT

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3.1 ABSTRACT

Aim: Although many studies have described and explained spatial patterns along elevational gradients, only a handful have investigated their temporal dynamics, which remains poorly understood. Here we investigate the patterns of frog spatiotemporal diversity (Anuran: Amphibia) along a subtropical elevational gradient, and assess the importance of temperature in explaining observed patterns.

Location: An extensive Brazilian Atlantic Forest elevational gradient ranging from 300 to 1,800 m above sea level.

Taxon: Anuran amphibians.

Methods: We sampled anurans once each month, between September 2017 and August 2018, at 38 ponds along the gradient. We then applied generalized additive models to evaluate the spatiotemporal patterns of frog diversity (measured as Hill's numbers of order $q = 0$, 1 and 2) and abundance, and understand of the extent to which this variation is explained by mean monthly temperature.

Results: We found seasonal changes in the shape and magnitude of frog diversity along the elevational gradient. While frog diversity showed mid-elevation peaks between spring and summer, a low-to-mid elevation plateau was observed during autumn and winter. Abundance peaked at mid-elevations between spring and summer, and was high through lowlands and decreased towards highlands between autumn and winter. Overall, frog diversity and abundance increased from spring to summer and then sharply declined towards winter, showing a nonlinear positive relationship with mean temperature. Temperature accounted for most of the observed spatial and spatiotemporal variation, but not temporal trends in frog diversity and abundance.

Main conclusions: Our results suggest that in addition to temperature, other factors such as intrinsic species characteristics may regulate anuran activity patterns throughout the year along the elevational gradient. This study highlights how local frog diversity is dynamic across the elevational gradient, emphasizing the relevance of considering seasonality to better understand diversity patterns in montane environments, which can be critical to inform conservation strategies.

Keywords: Altitudinal gradient, Atlantic Forest, frogs, Neotropcis, seasonality, space, species diversity, temperature.

3.2 INTRODUCTION

Understanding the patterns and processes behind distribution of biodiversity through space and time is a central goal in ecology and biogeography. This knowledge can be vital for management and effective conservation strategies, specially concerning montane regions (Díaz et al., 2019). Mountains around the world are biodiversity hotspots and harbour almost 90% of all known species of amphibians, birds and mammals, many of which are endemic to these regions (Körner, 2004; Rahbek et al., 2019). However, this astonishing diversity is at risk because montane ecosystems are predicted to be strongly affected by higher rates of climatic changes (Guisan et al., 2019; Pachauri et al., 2014). Consequently, there is an urgent need to understand the mechanisms shaping the structure and composition of natural communities in montane environments, creating baselines to detect how these systems may respond to climate change (Cowell & Rangel, 2010; Lomolino, 2001).

Elevational gradients on montane slopes are excellent systems to investigate biodiversity patterns given their rapid rates of climatic and environmental change over relatively short distances (Graham et al., 2014; Körner, 2007), which can affect species distribution and abundance. Studies concerning elevational gradients have therefore rapidly increased over the last decades (Fontana et al., 2020; Peters et al., 2016; Rahbek, 2005). Species diversity along these gradients can be distributed in different ways and vary across study regions and taxa, but a linear decline with elevation and mid-elevational peaks are the two most pervasive observed patterns (McCain & Grytnes, 2010; Peters et al., 2016). Many mechanisms have been suggested to explain these patterns, which generally invoke spatial, climatic, biotic, and evolutionary processes (Graham et al., 2014; Rahbeck et al., 2019).

However, intra-annual temporal variability (i.e. seasonality) in environmental conditions (e.g. precipitation, temperature) can strongly shape life history adaptations, species abundance, diversity and community assembly at multiple scales (Pianka, 1966; Schoener, 1974; Tonkin et al., 2017). These changes can influence species' activities, which may reflect physiological constraints, predator avoidance, resource tracking, and/or resource partitioning (Bradshaw & Holzapfel, 2007; Tonkin et al., 2017). For example, rainfall seasonality affects resource availability, imposing changes in the diversity and structure of many assemblages of tropical animals and plants (Condit et al., 2013; Grøtan et al., 2014). On the other hand, subtropical and temperate biotas have long been subjected to marked temperature seasonality, predisposing species to specific physiological adaptations to cope with harsh cold seasons, including spatial tracking of more favourable conditions (Ge et al., 2019; Wu et al., 2013). Furthermore, the interaction between elevation and seasonality as determinants of community structure has so far been poorly explored (Bishop et al., 2014; Maicher et al., 2020).

Despite these limitations, there is evidence that seasonality plays an important rule in shaping diversity patterns along mountain ridges (Bishop et al., 2014; Maicher et al., 2020). For instance, species richness of non-volant small mammals peaks at mid-elevations but this peak shifts to higher elevations between the dry and wet seasons (McCain, 2004). On the other hand, an opposite pattern was observed for tropical ants (Bishop et al., 2014). Moths in mid-latitude regions respond to seasonal changes in temperature, showing a linear decline in diversity at higher elevations during the autumn, which changes to a mid-elevation peak during the summer (Beck et al., 2010). These results suggest that combining spatial and temporal scales can contribute to a better understanding of how faunal diversity changes along elevational gradients.

Anuran amphibians (i.e. frogs and toads; hereafter, frogs) are megadiverse (7,463 species; Frost, 2021) and a highly threatened group of vertebrates (~ 40% of all amphibians are on the edge of extinction; Ceballos et al., 2020; IUCN, 2021). The high sensitivity of frogs to environmental change (Dickinson et al., 2014), render them suitable organisms to study diversity patterns. Previous studies indicate that mid-elevation diversity peaks (Fu et al., 2006; McCain & Sanders, 2010; Meza-Joya & Torres, 2016) and declining diversity at increasingly higher altitudes (Khatiwada et al., 2019; Siqueira et al., 2021) are the most common elevational patterns found in frogs. As ectotherms, climatic conditions, including rainfall, temperature and humidity, can strongly influence anuran physiology, and activities such as locomotion, foraging, and courtship (Angilleta et al., 2009; Navas et al., 2008). Higher species richness and abundance are generally found during the wet and/or warm seasons, which coincide with periods during which most frog species breed (Duellman & Trueb, 1994; Silva et al., 2012). However, temporal variation in frog elevational diversity has scarcely been investigated (Sun et al., 2021; Zhu et al., 2020), especially in the Neotropics. Anurans must exhibit ecological, behavioural and/or physiological adaptations to maintain vital activities under low body temperatures, which they typically experience during winters in high-elevation areas (Huey, 1982; Navas, 2006).

Our aim here was investgate the spatiotemporal dynamics of frog diversity along an extensive subtropical elevational gradient in the Brazilian Atlantic Forest (Figure 1a). Our previous study in the same meta-landscape showed that frog species richness peaked at mid-elevations, whereas frog abundance showed a low-elevation plateau when year-round monthly data are pooled for all sites (Carvalho-Rocha et al., 2021). We now addressed two complementary questions: (i) what is the degree of seasonal variation in elevational patterns of frog diversity? and (ii) how much of these patterns can be explained by changes in temperature? We predicted that the form of these relationships would change throughout the year in line with previous studies on seasonal montane systems (Bishop et al., 2014; Maicher et al., 2019). As temperature can strongly influence anuran activity and physiology, we expected to find a positive relationship between frog diversity and temperature. Given that low elevations experience milder reductions in temperature during winters compared to high elevations, we expected that the interaction between elevation and season would shape patterns of frog diversity. As a consequence, these patterns would be largely explained by local variation in temperature.

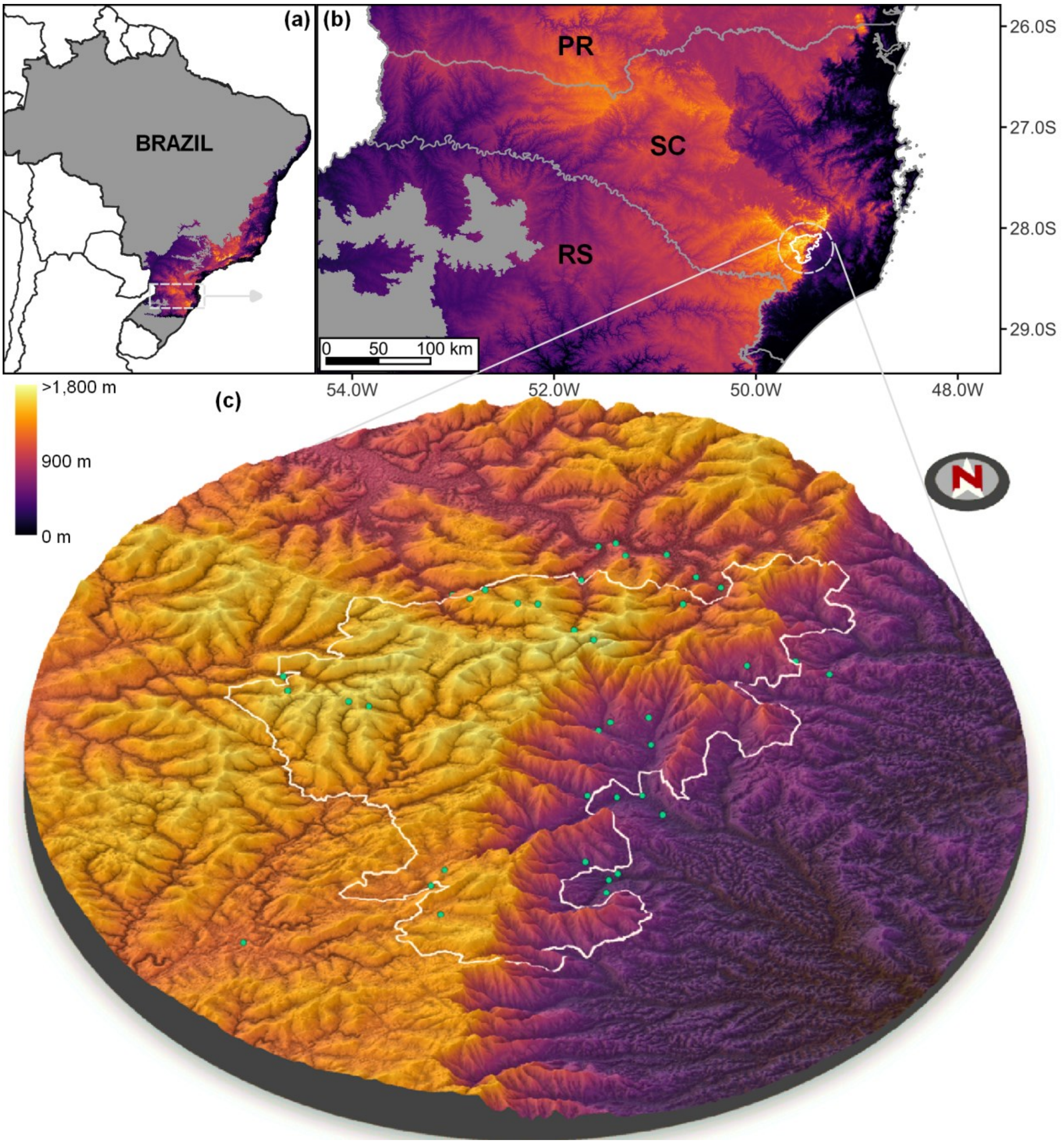

Figure 1. Map of study area and location of sampled ponds. (a) Extension of the Brazilian Atlantic Forest, with (b) its southern portion highlighted showing the location of the São Joaquim National Park (SJNP) at Santa Catarina State. (c) 3D relief map of the the SJNP (white line) and surrounds depicting the elevational gradient and distribution of the 38 sampled ponds (green dots). The colour gradient in (a), (b) and (c) indicates elevation in meters above sea level and follows the same scale depicted in (c). PR: Paraná; RS: Rio Grande do Sul; SC: Santa Catarina.

3.3 MATHERIALS AND METHODS

3.3.1 Study site

The data was collected within the complex mountainous landscape of Serra Geral formation, which has ~920,000 km² and extends from Argentina through Uruguay, Paraguay and southern to south-eastern Brazil (Frank et al., 2009). We selected an extensive elevational gradient within the São Joaquim National Park and its vicinities, which is a ~49,800 ha strictly protected area located in the state of Santa Catarina, southern Brazil (Figure 1b-c). This area is insert into the Atlantic Forest, a biome considered one of the hottest biodiversity hotspots of the world (Myers et al., 2000), with only 26% of its original forest cover remaining (Rezende et al., 2018). The selected region encompasses ~1,200 km² of dissected terrain with elevations ranging from 200 m to 1,822 m above sea level (de Vianna et al., 2015). Dense evergreen forest cover areas up to 800 m, which is gradually replaced by mixed Araucaria forest and high-altitude grasslands at higher elevations (IBGE, 2012). The local humid subtropical climate has no dry season and interacts with elevation: summers are hot and mean annual temperature is 19°C below 800 m, whereas at mid to high-elevations (> 800 m), winters are cold, with frequent frosts, and the mean annual temperature is 13.5°C (Alvares et al., 2014).

3.3.2 Sampling design and data collection

We selected 38 discrete permanent lentic aquatic environments (ponds, humid areas, marshes and small dams; hereafter, ponds), which are considered suitable areas to find most Atlantic Forest frog species as they use these areas and their vicinities to reproduce and forage (Crump, 2015; Haddad et al., 2013). Chosen ponds were situated at elevations between 312 m and 1,798 m, distributed irregularly within this range, but not biased for or against any single region (i.e. elevational bands) of the gradient (McCain & Grytnes, 2010). Lower elevation areas, although available, were disregarded because they are heavily human-altered in the studied region. Pond selection also accounted for sufficient spatial independence between them based on the overall dispersal capability of frogs (~1 km of minimum distance between ponds; Gagné & Fahrig 2007). The detailed protocol used here to select the ponds can be found in Carvalho-Rocha et al. (2021). See Appendix S1 Table S1.1 in Supplementary Information for a description of the selected ponds.

We sampled frogs monthly at each pond, between September 2017 and August 2018, encompassing one southern hemisphere seasonal cycle. Unfortunately, surveys could not be done during December 2017 and April 2018, leaving us with a total of 10 sampled months. We searched for frogs combining visual and acoustic encounter surveys within a 5-m buffer along pond perimeter in order to maximize visual and acoustic anuran detectability and simultaneously avoiding double counting individuals (Heyer et al., 2014). Surveys always initiated at least one hour after dusk and ended no later than 01:00 hr, interval where most frog species are active (Guerra et al., 2020). Search effort was also standardized by one person-hour per pond per month. Pond survey sequence was randomized across months to minimize any bias related to nocturnal sampling schedules. Two voucher individuals per species per pond were collected, when possible, under research permit previously granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, permit #59223-1), and were deposited at the Universidade Federal de Santa Catarina Herpetological Collection, Brazil.

Due to budget constraints, we could not afford data loggers to be allocated at each pond. Instead, we measured the air temperature with a digital thermometer (°C; Inconterm 7,664®; one meter above the ground) at each pond during surveys. We averaged the values registered at the start and at the end of surveys and considered this value as the mean observed temperature (hereafter, T_{obs}). We acknowledge that this approach may not reflect the overall seasonal variation in temperatures experienced by the frogs. Therefore, we also estimated the mean monthly temperature for each pond (hereafter, T_{mean}). For that, we used NASA's daily land-surface temperature product MOD11A2.006 (~1 km^2 spatial resolution; Wan, 2014) and extracted the values within our sampled period (i.e from September 2017 to August 2018). Next, we calculated, for each day, the mean pixel values within a ± 50 m vertical elevation buffer based on each ponds' centroid. Total area was limited by a 50-km horizontal radius from the highest mountain across our study region (McCain, 2007). This framework is analogous to the 100-m elevation band commonly used in other elevational gradient studies (e.g. Beck et al., 2017). Finally, T_{mean} was estimated as the average of all days within each sampled month. Procedures to obtain T_{mean} ware done using Google Earth's Engine cloud computing platform (www.code.earthengine.google.com).

3.3.3 Statistical analysis

Our spatiotemporal analytical approach was developed considering frog abundance and diversity at the 380 sampled assemblages (i.e., 38 ponds x 10 months). Initially, we assessed our data reliability by evaluating sample completeness by means of abundance-based sample coverage using the "iNEXT" R package (Hsieh et al., 2016). All subsequent analyses were also done in R software (R Core Team, 2021). Frog abundance represented the total number of individuals registered per pond per month. Frog diversity was quantified using the Hill's numbers framework (${}^{q}D$), which measures the effective number of species on the assemblages (i.e. the equivalent number of equally abundant species; Hill, 1973). Hill's numbers are parametrized by a diversity order q that regulates the sensitivity of species abundance (Chao et al., 2014). We selected Hill's ${}^{q}D$ of order q = 0, 1, and 2 to represent different levels of frog diversity. The Hill number ${}^{0}D$ disregards species abundance and corresponds to species richness (i.e. emphasize the rare species). For ${}^{1}D$, species are weighed in proportion to their abundances and is equivalent to Shannon diversity (i.e. the exponent of Shannon entropy), been interpreted as the effective number of common species. When ^{2}D, rare species are discounted and abundant species are favoured, and the index is reduced to Simpson diversity (i.e. inverse Simpson's concentration index), which can be interpreted as the effective number of dominant species (see Chao et al. (2014) for details on indices calculation). We also estimated ${}^{0}D$, ${}^{1}D$, and ${}^{2}D$ using the "iNEXT" package (Hsieh et al., 2016), and used Spearman's rank-order to examine the correlation between observed and estimated diversity values.

We used generalized additive models (GAMs) to answer our two main questions. GAMs are a flexible, nonparametric technique that use penalized regression splines to fit smooth relationships between response and predictors variables (Wood, 2017). To evaluate seasonality in elevational diversity patterns of frogs (our first question), we built individual spatiotemporal models for ${}^{0}D$, ${}^{1}D$, ${}^{2}D$, and abundance. These models included as fixed terms: a marginal smooth of elevation, a marginal smooth of month (i.e. seasonal variation, expressed as numeric from the first sampled month: September = 1, October = 2, …, August = 12; Telesca et al., 2021), and a tensor product interaction of elevation and month. A tensor product interaction is suitable to represent functions of covariates that are measured in different units (i.e. have different magnitude of change), allowing, for this case, the smooth effect of elevation to vary as a smooth function of month (Wood, 2017). We accounted for the dependency among observations from the same pond by including pond id as a random factor in the models. A thin plate regression spline basis was used to fit the elevation smooth, whereas a cyclic cube spline was used for the seasonal smooth term to capture any cyclic pattern and avoid any discontinuity between August and September. We used a negative binomial distribution (count data) for abundance and ${}^{0}D$, and a Tweedie distribution (zero-inclusive, positive, continuous responses) for ${}^{1}D$ and ${}^{2}D$, all with a log-link function. We applied the double penalty approach, which allows for terms that are not related to the response to be effectively removed from GAMs, meaning that terms that had estimated degree of freedom shrunk approximately to zero had negligible contribution to model fit (Marra & Wood, 2011).

We also accounted for any spatial autocorrelation in our data. For that, we built a second model just like the previously described, but also included a smooth interaction term of pond's coordinates (i.e. longitude and latitude) with a Gaussian process spline to account for any unspecified spatial structure (Wood, 2017; Ziter et al., 2019). We then compared the difference of Akaike information criterion (AIC) of these two sets of models. Coordinates were kept in the model only if they lowered the AIC by at least two units, indicating improvement in model fit (Burnham & Anderson, 2004); otherwise, spatial autocorrelation was considered negligible.

Next, we used a two-step procedure to answer our second question, i.e. the importance of temperature in explaining the spatiotemporal patterns depicted in our first set of models (Bishop et al. 2014). In the first step, we built GAMs including only temperature and pond id as predictors of frog diversity and abundance. The smooth of temperature was fitted with a thin plate regression spline, and a negative binomial distribution was used for ${}^{0}D$, and abundance, while a Tweedie distribution was used for ${}^{1}D$ and ${}^{2}D$. Pond id was also included to control for repeated measures, and we also evaluated the presence of spatial autocorrelation as previously described. Because our temperature measures were strongly correlated (Spearman's rho = 0.69; S = 2804328; p-value < 2.2e-16), we fit separated models for T_{obs} and T_{mean}. Overall, T_{mean} had a better fit than T_{obs} (Appendix S1 Table S1.2), and we only kept the first in our further analysis. The second step then consisted in evaluate if there were any spatiotemporal patterns remaining in the residuals of ${}^{0}D$, ${}^{1}D$, ${}^{2}D$ and abundance after accounted for the effect of temperature. For that, we modelled these residuals using the same set of predictors and model structure used to evaluate the spatiotemporal patterns in our first question. But now, models included a Gaussian (identity link) error distribution. GAMs were fitted with the R package “mgcv” (Wood, 2018) with automatic smoothness estimation using Restricted Maximum Likelihood.

3.4 RESULTS

We registered 12,626 individuals from 40 frog species and nine families (Table S1.3). The higher total number of species (${}^{0}D$) observed during surveys at a pond was 12, both at 991 m in the austral mid-spring (October 2017), and at 621 m in mid-summer (January 2018). The higher effective number of common species (${}^{1}D$) and abundant species (${}^{2}D$) were 9.76 and 8.87, respectively, and they were both observed at 1,330 m in late spring (November 2017). Maximum frog abundance was 313, and it was observed at a pond located at 1,337 m, also in late spring. From 380 visits at ponds (i.e. 38 ponds x 10 sampled months), we found no frogs in 74 of them (~20 %). Most absences were in early winter (June 2018), in which 25 of 38 ponds lacked frogs (See figure S2.1). Mean observed temperature (T_{obs}) during surveys ranged from 22.2°C at 1,118 m in late spring, to -2.8°C at 1,633 m in late winter (August 2018), whereas mean monthly temperature (T_{mean}) ranged from 22.68°C at 312 m in mid-summer, to 9.37°C at 1546 m in early winter (Figure S2.2). Overall, sample coverage was high (mean = 0.964; SD = 0.008; median = 1; Figure S2.3), and observed and estimated frog diversity were highly correlated (Spearman's rho values > 0.93 for all ${}^{0}D$, ${}^{1}D$, and ${}^{2}D$; Figure S2.4). Accordingly, we used the observed values in all subsequent analysis.

As expected, our first set of GAMs suggested the presence of strong spatiotemporal patterns in frog diversity and abundance. Models including elevation, season and their interaction explained 68%, 61.3%, 56.5% and 66.4% of the deviance in ${}^{0}D$, ${}^{1}D$, ${}^{2}D$, and abundance, respectively (all smooth terms p-value ≤ 0.0012; Table S1.4). Considering the partial effect of elevation, all metrics of frog diversity showed a low-to-mid elevation plateau pattern, which corresponded to overall high values up to roughly 900 m that decreased towards higher elevations (Figure 2a-c; Table S1.4). In contrast, frog abundance showed an almost linear decline considering the partial effect of elevation (Figure 2d; Table S1.4). The partial effect of sampled month suggested a pronounced seasonal cyclic pattern for both frog diversity and abundance. Values increased from early spring to early summer (September to December), where they peak, and then sharply declined towards early winter (June). From mid to late winter (July to August), values started increase back again (Figures 2e-h; Table S1.4).

When space and time are jointly considered, GAMs' predictions suggested that the shape and magnitude of frog diversity and abundance along the elevational gradient changed seasonally (Figure 3). For frog species richness (${}^{0}D$), the seasonal patterns can be roughly described as a low-to-mid elevations plateau for the most part of the year, which changed to a low plateau with a peak at mid-elevations during late spring and early summer (Figure 3a). From spring to winter, the low-to-mid elevations plateaus not only got shorter, with values start decreasing at lower elevations, but also got smaller, with lower maximum values. On the other hand, the mid-elevation peak is more pronounced during the early summer then late spring (Figure 3a). We observed virtually the same overall patterns for both the effective number of common (${}^{1}D$, Figure 3b) and dominant species (${}^{2}D$; Figure 3c). The major difference was that the effective number of dominant species only showed low-to-mid elevations plateau pattern. Frog abundance, on the other hand, peaked at intermediate elevations along spring and summer months, but values were higher and peaked at lower elevations in summer. Overall, values increased from early spring to early summer and then decreased towards winter. Abundance patterns in Autumn can be described as a low-elevations plateau, and fewer individuals were found. During early and mid-winter, the lower values were found across the whole elevational gradient, but became increase again at lower elevations during late winter (Figure 3d). Including ponds coordinates neither improved models' fit nor increased deviance explained, suggesting no evidence of spatial autocorrelation in our data (Table S1.5).

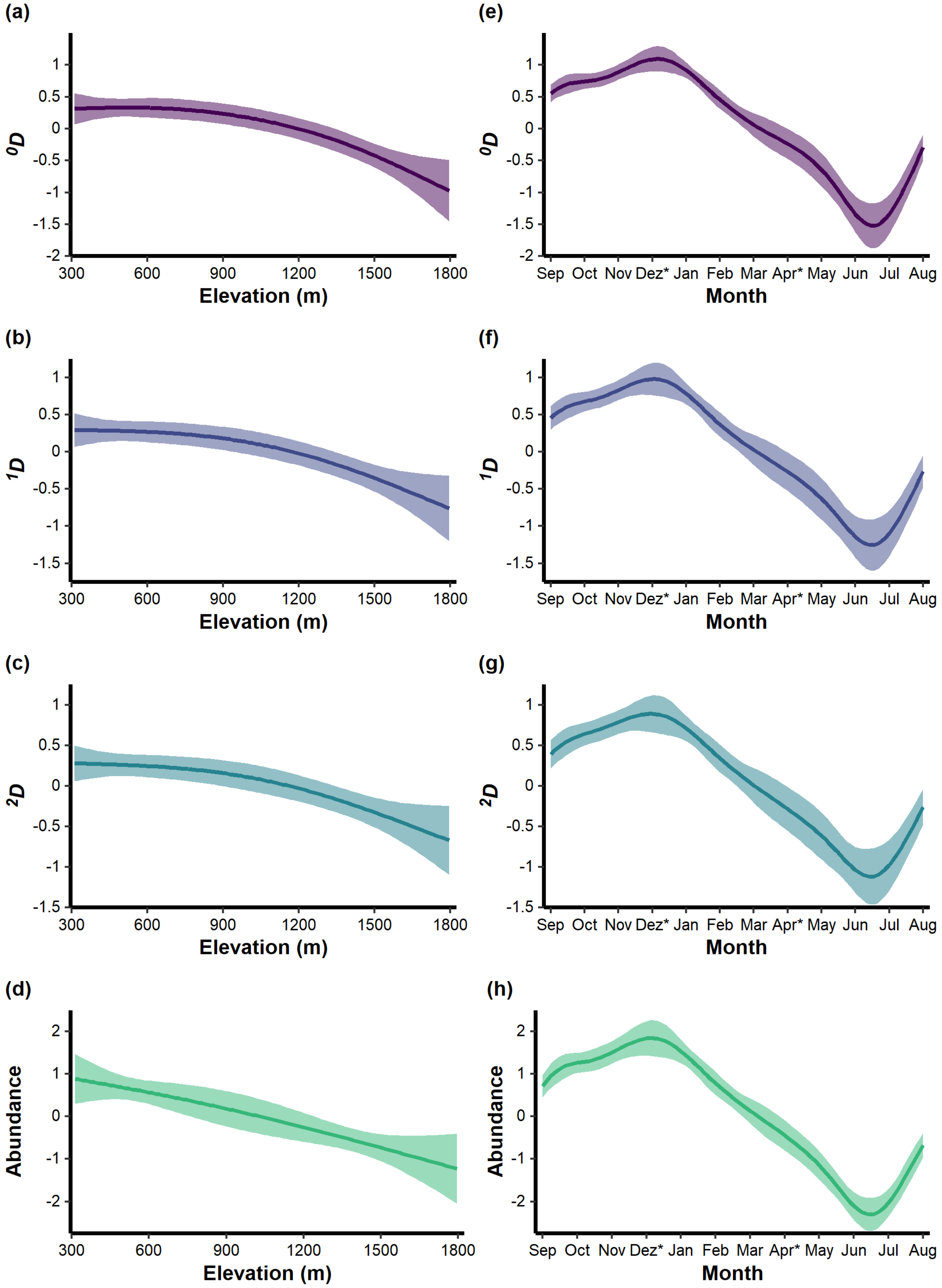

Figure 2. Modeled marginal smooth effects of elevation (a-d) and season (e-h) on frog diversity (^{q}D of order q = 0, 1, and 2) and abundance in 38 ponds along the São Joaquim National Park and surrounding areas, southern Brazil. Lines represent the mean effect and shaded areas are 95% credible intervals. Note that *x*-axis in centered at zero and have different scale for each

response variable. See Table S1.4 for detailed models. *Months not sampled but values were estimated through the models.

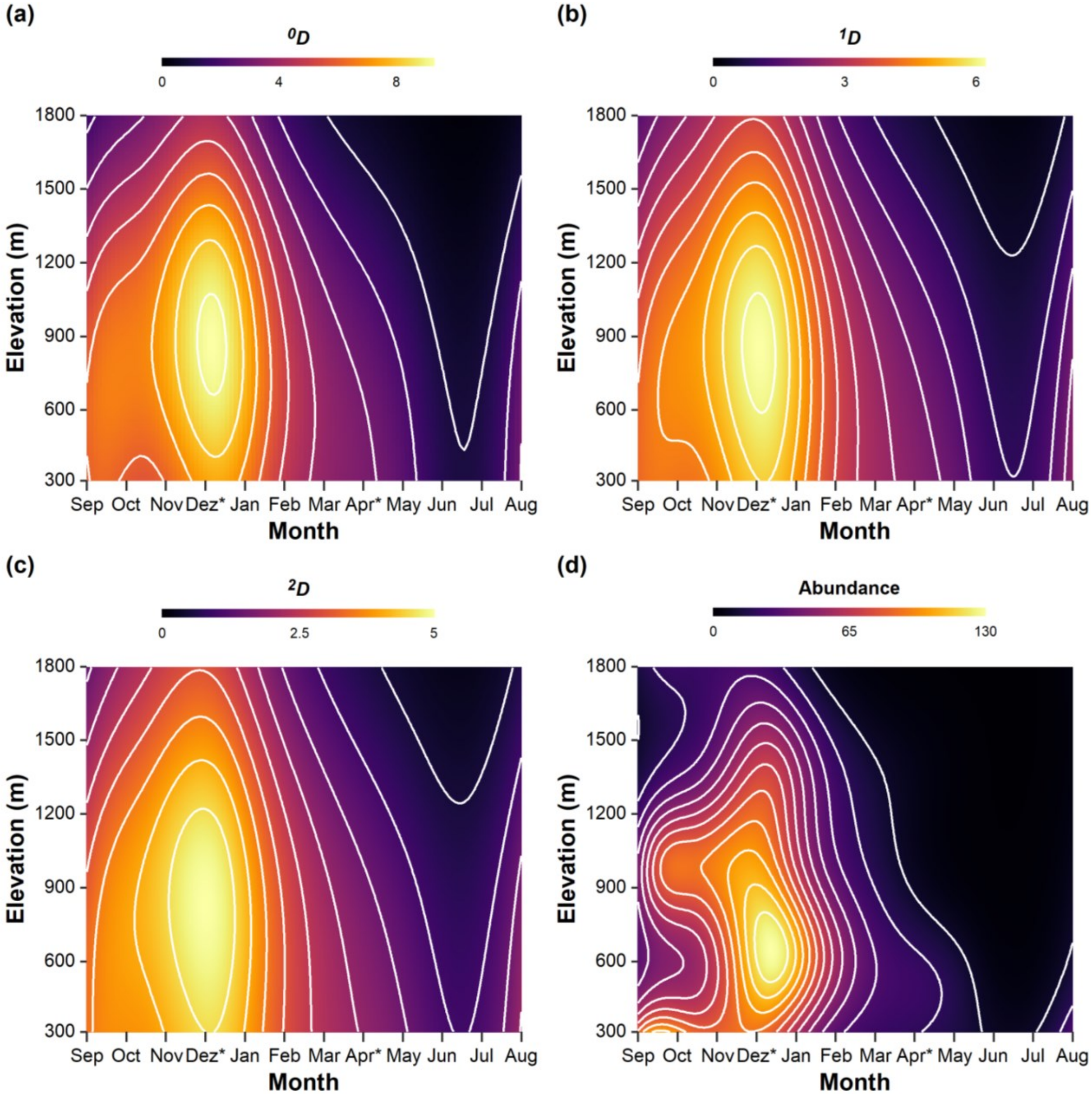

Figure 3. The spatiotemporal patterns of frog diversity and abudnance along the studied elevational gradient at the São Joaquim National Park and surrounding areas, southern Brazil. Contour plots show predicted values derived from the generalized additive models for frog diversity (^qD of order q = 0, 1, and 2; a-c) and abundance (d). Note the different colour scales highlighting differences in the magnitude of change for each response variable. Lines represet 1, 0.5, 0.5, and 10 units change in ^0D, ^1D, ^2D, and abundance, respectively. *Months not sampled but estimated through the models.

Models that included only the mean monthly temperature (T_{mean}) as a predictor suggested a non-linear positive relationship with ^0D, ^1D, ^2D and frog abundance (temperature smooth term p-value < 2e-16 for all responses), which explained 57.6%, 52.1%, 47.9% and 55.7% of their deviance, respectively (Figure 4; Table S1.3). We also found no evidence of spatial autocorrelation (Table S1.5). To answer our second question, we then used the residuals of these aforementioned models and tested for any spatiotemporal patterns left. We could find evidence of only residual seasonal variation (smooth of month p-value < 2e-16) in the residuals of ^0D, ^1D, and ^2D. These models explained 25.3%, 23% and 21% of their deviance, respectively (Table S1.3). These results suggest that the spatial and spatiotemporal patterns of frog diversity are explained by differences in mean monthly temperature. For frog abundance, although weaker, we still could find spatiotemporal patterns after accounted for the effect of temperature, with model explaining 27.3% of the deviance (Table S1.3).

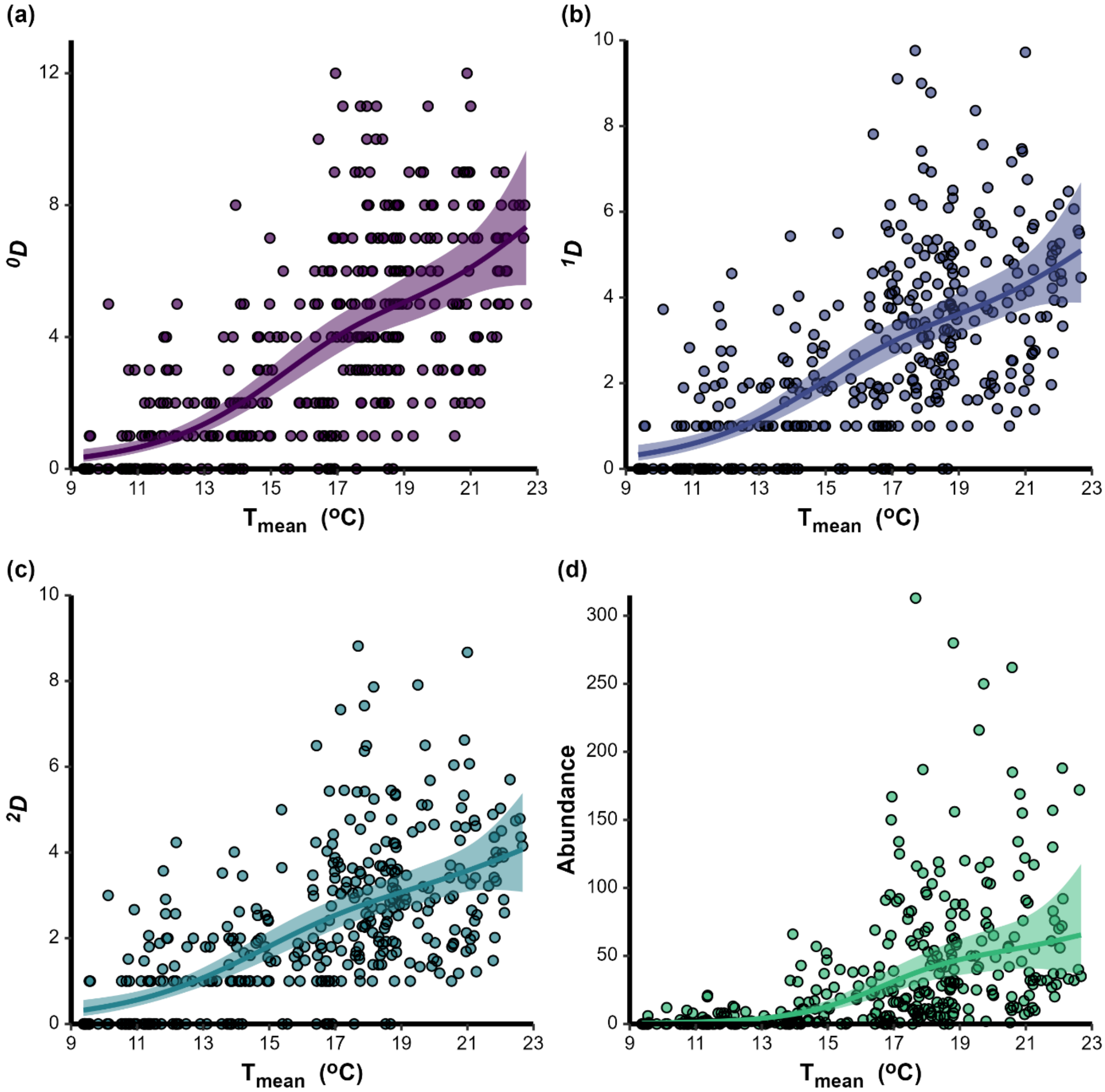

Figure 4. The modeled predicted effects of mean monthly temperature (T_{mean}) on frog diversity (^qD of order q = 0, 1, and 2; a-c) and abundance (b) along the São Joaquim National Park and surrounding areas, southern Brazil. Lines represent the predicted mean, shaded areas are 95% credible intervals and points are the 380 sampled frog assemblages (i.e., 38 ponds x 10 months).

Note differences in *x*-axis for the response variables. See Table S1.4 for detailed models` parameters. *Months not sampled but values were estimated through the models.

3.5 DISCUSSION

To the best of our knowledge, our study is the first to provide insights on how coupled spatial and temporal dimensions shape neotropical anuran diversity along a complete subtropical elevational gradient. As predicted, elevational patterns of frog diversity (all measures of ${}^{0}D$, ${}^{1}D$ and ${}^{2}D$) and abundance changed seasonally. All of these metrics also showed a strong positive relationship with mean monthly temperature. Most of the spatiotemporal patterns could also be explained by changes in mean monthly temperature, but some residual seasonal trends still remained. This suggests that elevational patterns in frog diversity are strongly dependent on temporal ecological constraints related to the seasonal variability in temperature.

The multiple year-round elevational patterns of frog diversity and abundance are consistent with those previously reported for other vertebrates and invertebrates occurring in seasonal montane regions (Bishop et al., 2014; Maicher et al., 2020; McCain, 2004; He et al., 2022). However, to our knowledge, only two previous studies have also investigated both the seasonal and elevational variations in frog diversity, both of which were conducted across the temperate Tianping Mountain in China (Sun et al., 2021; Zhu et al., 2020). In these studies, taxonomic diversity changed with elevation in two of the four sampled months (Zhu et al., 2020), but functional diversity did not vary among seasons (Sun et al., 2021). Elevational diversity patterns are known to vary both within and between a geographic region, even within a single taxon (McCain & Grytnes, 2010). Our data adds to the notion that seasonal variation is also an important factor to consider on studies concerning elevational diversity patterns (Beck et al., 2010; Maicher et al., 2019). In addition, we highlight that this seasonality can also occur in the subtropics, rather than only in temperate and tropical regions. Unfortunately, we are unable to propose explanatory generalizations given that only a few studies have attempted to describe such temporal variation in anurans.

When data across the entire annual cycle is pulled, frog diversity at our study sites showed a mid-elevation peak (Carvalho-Rocha et al., 2021). A linear decline or peak at intermediate elevations are the most frequently reported pattern of elevational diversity in frogs (Khatiwada et al., 2019; McCain & Sanders, 2010). However, breaking down samples into seasons (i.e. trimesters or months), we found that frog diversity for most of the year is similarly high up until mid-elevations at SJNP, but then declines further upslope in the highlands. These high-diversity peaks, however, change in magnitude; values increase from spring to summer (for all diversity metrics), but then decline towards the coldest months of the year. Elevations where diversity declines also changed, going from intermediate to lower elevations towards the winter. Mid-elevation peaks, although observed, were restricted to late-spring to mid-summer months. Such observed spatiotemporal variability is apparently related, at least partly, to the thermal niches of individual species. Residual models of frog diversity recovered a weak seasonal pattern, but only after the effect of mean temperature had been removed. This suggests that variation in mean temperature may play an important role in promoting not only overall elevational patterns, but also how these patterns change seasonally.

Abiotic conditions, such as temperature, that are strongly correlated with elevation, have been identified as the most important factors shaping the distribution of diversity at high elevations (Peters et al., 2016; Sanders & Rahbek, 2012). Temperature specifically is also considered an important spatial and temporal predictor of anuran diversity (Buckley & Jetz, 2007; Vasconcelos et al., 2019). As ectotherms, frogs rely heavily on ambient temperature to regulate their physiology, behaviour and performance (Navas et al., 2008). However, although our results showed that frog diversity has a positive relationship with mean monthly temperature, we found no evidence of a monotonic upslope decline in frog diversity, which would be predicted by a constant decline in temperature as elevation increases. Rather, our data suggests that local conditions become particularly harsher for anurans only above a certain threshold of mid-elevation temperatures, as similar diversity values were found along low-to-mid elevations. Subsequent declines in diversity above mid-elevations could be related to fewer co-occurring species bearing physiological adaptations to cope with colder temperatures. This in turn could explain the low-to-mid elevation plateaus observed. Indeed, a decrease in critical thermal limits along elevational gradients has been reported for anurans (von May et al., 2017) and other ectotherms (Gaston & Chown, 1999). However, we lack empirical data on the thermal tolerances of most anuran species, especially for those living across neotropical mountains (Navas et al., 2013; von May et al., 2017). Therefore, further studies are needed to investigate this hypothesis.

In markedly seasonal climates, anurans activity patterns are mainly regulated by variation in temperature and/or rainfall (Duelmann & Trueb, 1994). Within the study montane system, rainfall is well distributed throughout the year due to interception of orographic moisture, with total monthly cumulative values ranging from 116 mm to 189 mm (Gotado et al., 2018). However, temperature fluctuations show a marked seasonal pattern between hot summers and cold winters (Alvares et al., 2014). Therefore, as suggested by our models, the increase in frog diversity from spring to summer, followed by a decrease through winter, is most likely related to seasonal changes in temperature. Similar cyclic patterns were also observed for other subtropical regions (Bolzan et al., 2019; Ceron et al., 2020). As temperature increases through summer, higher elevations also become warmer and climatically suitable for larger numbers of species. On the other hand, cold snaps that are frequently accompanied by hard frosts during winter can be tolerated by only few cold adapted species, which led to sharper declines in overall species diversity and abundance throughout the entire elevational gradient.

Although early spring and early autumn experienced similar mean temperatures (Figure S2.2), frog diversity dropped roughly by half between the former and the latter, which is reflected in the residual seasonal patterns we found. Lower temperatures can not only constrain adult anurans, but also depress survival, development and growth rates of their eggs, tadpoles and juveniles (Benard, 2014; Hutchison & Dupré, 1992). Therefore, the observed step decline in frog diversity after the mid-summer period may suggest that most species depend on warmer temperatures to meet their reproductive requirements. Indeed, most species were active only during these warmer periods, but a few remained active throughout the year (e.g. *Boana bischoffi*, *Leptodactylus latrans*; Figure S2.1), irrespectively of whether they were elevation generalists or specialists. However, even those species showed different activity patterns across the elevational gradient. At sites above mid-elevations, their highest abundances were restricted to the summer months, whereas at lower elevations, those same species were found in good numbers all year-round (Figure S2.1). Our results emphasize the role of physiological constraints imposed by a key dimension of environmental conditions (i.e. temperature) in shaping patterns of anuran diversity throughout subtropical elevational gradients.

Unlike for the diversity metrics quantified here, mean monthly temperature poorly explains the seasonal changes in frog abundance along the elevational gradient. Considering the general temporal patterns, cold snaps could also explain the small numbers of frogs during the winter months, as previously stated for species diversity. The high frog abundance at intermediate elevations during warm months of the year is likely related to food availability. The abundance of arthropods, which comprise the bulk of the diet of anurans (Carvalho-Rocha et al., 2018; Solé & Rödder, 2010), also generally peaks at intermediate elevations in seasonal mountains (e.g. Bishop et al., 2014; Peters et al., 2016), and is related to their synchronous emergence due to short growing seasons (Pilar et al., 2020). As in most organisms, information on patterns of arthropod diversity and abundance in montane Atlantic Forest environments is limited, but available data, including in our study landscape (da Silva et al., 2018), suggest mid-elevational peaks (Araújo et al., 2021). Therefore, intermediate elevations could harbour more food resources and support more individuals (Srivastava & Lawton, 1998), thereby partly explaining the observed patterns. However, we failed to quantify the seasonality of food resource availability, which should be addressed in future studies to assess these proposed mechanisms.

Studies that aim to evaluate seasonality in diversity patterns along elevational gradients generally focus on characterizing the most climatic divergent periods, with samples usually collected during the rainy/hot and dry/cold seasons (e.g. McCain, 2004; Munyai & Foord, 2015). However, seasonality implies cyclical changes in environmental conditions which usually occur gradually over time (Tonkin et al., 2017). Detailed studies with multiple samples obtained throughout the annual cycle, such as this study, are scarce, and studies over multiple years are even scarcer (but see Bishop et al., 2014; He et al., 2021; Nunes et al., 2020). We acknowledge that multi-year replicates would ensure a better understanding of the generality of the trends observed here. Nonetheless, this does not invalidate the results presented here, as we stress the importance of using monthly inventory data to better understand the mechanisms driving seasonal patterns of biotic diversity across sharp spatial gradients.

Rapid climate change at regional to global scales is now affecting all organisms (Steinbauer et al., 2018). Montane regions are facing a disproportionate increase in temperatures compared to other ecosystems, and both predictive and empirical studies point to wholesale changes in the distribution ranges of many disparate taxa (Freeman et al., 2018; Tagliari et al. 2021), including frogs (Kusrini et al., 2017; Tiberti et al., 2021). Species with narrow thermal tolerances, particularly those restricted to mid and high elevations, are of most concern as warming microclimates leave little or no suitable habitats to track these changes. Given growing numbers of reports indicating regime shifts in seasonal precipitation and temperature (Gilford et al., 2017), there is an urgent need to improve our knowledge on the seasonal dynamics of ectotherm vertebrate diversity along elevational gradients. This is an important step to recognize vulnerable species under the current scenario of climate change, but also those that can possibly cope with these climate regime shifts. Our findings are then relevant as they can be used as baseline to track changes in frog diversity and help design effective conservation strategies as climate change modify the environment of montane landscapes.

To conclude, our study highlights the importance of temperature in regulating the spatiotemporal patterns of neotropical anuran diversity along a sharp elevational gradient. Understanding how community dynamics are structured at varying spatial and temporal scales is the first step in improving our current knowledge and testing ecological theories. This can also be used to guide successful conservation strategies confronting the often co-occurring processes of land use and climate change in tropical mountains.

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3.8 SUPPLEMENTARY INFORMATION

Supplementary information for

SEASONAL VARIATION IN PATTERNS OF ANURAN DIVERSITY ALONG A SUBTROPICAL ELEVATIONAL GRADIENT

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APPENDIX S1. Additional tables.

TABLE S1.1. Identity codes (ID), geographic position centroids (degrees), elevation (meters above sea level) and surface area (m²) of the 38 surveyed ponds at São Joaquim National Park (SJNP) and surrounds, Santa Catarina, Brazil.

Pond ID	Longitude	Latitude	Elevation	Surface area
P01	-49.475843	-28.27096	312	1014.43
P02	-49.471251	-28.266882	322	6691.03
P03	-49.448269	-28.22512	328	1886.05
P04	-49.458121	-28.21171	352	688.18
P05	-49.470778	-28.213213	384	553.89
P06	-49.45317	-28.177236	442	947.28
P07	-49.477235	-28.282905	465	1226.36
P08	-49.485467	-28.213576	475	1854.6
P09	-49.487366	-28.261007	477	845.52
P10	-49.363367	-28.130717	571	5300.75
P11	-49.454128	-28.160606	601	2249.38
P12	-49.473162	-28.164016	621	6722.97
P13	-49.479192	-28.170122	639	911.65
P14	-49.404297	-28.126418	708	3276.79
P15	-49.380148	-28.123942	712	835.98
P16	-49.476978	-28.043779	929	1202.78
P17	-49.443083	-28.051046	958	209.32
P18	-49.416454	-28.075432	983	2381.7
P19	-49.42869	-28.067771	985	538.16
P20	-49.485991	-28.069147	991	222.6
P21	-49.468315	-28.043531	1024	1551.63
P22	-49.463754	-28.054644	1131	718.91
P23	-49.550437	-28.081191	1139	4325.45
P24	-49.658752	-28.329245	1198	780.89
P25	-49.564759	-28.292319	1303	675.89
P26	-49.557812	-28.281763	1330	5989.96
P27	-49.435689	-28.093822	1337	524.94
P28	-49.63574	-28.142349	1353	595.23
P29	-49.560454	-28.314437	1373	422.23
P30	-49.534131	-28.083537	1425	720.88
P31	-49.541867	-28.089954	1444	735.18
P32	-49.490391	-28.11551	1546	356.93
P33	-49.633818	-28.156881	1575	552.05
P34	-49.593613	-28.168796	1586	351.53
P35	-49.603651	-28.165981	1627	475.68
P36	-49.518134	-28.097339	1633	13547.38
P37	-49.508118	-28.09821	1636	415.93
P38	-49.480814	-28.127386	1796	522.08

Table S1.2. Summary of generalized additive models used to assess the relationship of frog diversity (measured as Hill's numbers ${}^{q}D$ of order q = 0, 1, and 2) and abundance as a function of mean observed temperature (T_{obs}) and mean monthly temperature (T_{mean}). Models are ranked by ΔAIC, with values < 2 indicating equally well supported.

Response	**Model type**	**Deviance explained (%)**	**edf**	**AIC**	**ΔAIC**
${}^{0}D$	T_{obs}	39.7	23.25	1640.432	135.145
	T_{mean}	57.6	31.72	1505.287	0
${}^{1}D$	T_{obs}	36.6	26.06	1349.961	113.642
	T_{mean}	52.1	28.54	1236.319	0
${}^{2}D$	T_{obs}	32.8	20.86	1278.369	83.224
	T_{mean}	47.9	24.44	1195.145	0
Abundance	T_{obs}	41.2	29.04	3052.799	106.3
	T_{mean}	55.7	32.83	2946.499	0

Table S1.3. Fog species, abbreviated names, minimum and maximum registered elevation and their total abundance among the 38 ponds surveyed between September 2017 and August 2018 at SJNP and surrounds, Santa Catarina, Brazil.

Family	Species	Abbreviation	Minimum elevation	Maximum elevation	Total Abundance
Brachycephalidae					
	Ischnocnema henselii (Peters, 1870)	I.hen	621	712	5
	Ischnocnema aff. *manezinho*	I.man	1337	1337	1
Bufonidae					
	Rhinella henselii (Lutz, 1934)	R.hen	983	1024	20
	Rhinella icterica (Spix, 1824)	R.ict	312	1796	528
	Rhinella ornata (Spix, 1824)	R.orn	322	708	23
Hemiphractidae					
	Fritziana mitus Walker, Wachlevski, Nogueira da Costa, Nogueira-Costa, Garcia, and Haddad, 2018	F.mit	571	571	6
Hylidae					
	Aplastodiscus perviridis Lutz, 1950	A.per	712	1633	120
	Boana bischoffi (Boulenger, 1887)	B.bis	312	1636	3022
	Boana faber (Wied-Neuwied, 1821)	B.fab	321	1337	552
	Boana joaquini (Lutz, 1968)	B.joa	983	1546	209
	Boana leptolineata (Braun and Braun, 1977)	B.lep	621	1796	259
	Boana marginata (Boulenger, 1887)	B.mar	621	621	3
	Boana prasina (Burmeister, 1856)	B.pra	621	1636	142
	Dendropsophus microps (Peters, 1872)	D.mic	322	1444	356
	Dendropsophus minutus (Peters, 1872)	D.min	621	1796	1674
	Dendropsophus nahdereri (Lutz and Bokermann, 1963)	D.nah	322	1796	277
	Pseudis cardosoi Kwet, 2000	P.car	1131	1373	190
	Scinax argyreornatus (Miranda-Ribeiro, 1926)	S.arg	712	712	2
	Scinax berthae (Barrio, 1962)	S.ber	958	1636	106
	Scinax catharinae (Boulenger, 1888)	S.cat	1337	1546	96
	Scinax fuscovarius (Lutz, 1925)	S.fus	465	708	124

	Scinax granulatus (Peters, 1871)	S.gra	991	1796	198
	Scinax perereca Pombal, Haddad, and Kasahara, 1995	S.per	312	1546	833
	Scinax rizibilis (Bokermann, 1964)	S.riz	475	712	50
	Scinax squalirostris (Lutz, 1925)	S.squ	991	1796	52
	Scinax tymbamirim Nunes, Kwet, and Pombal, 2012	S.tym	312	621	801
	Sphaenorhynchus surdus (Cochran, 1953)	S.sur	322	1636	353
	Trachycephalus dibernardoi Kwet and Solé, 2008	T.dib	1425	1444	4
Hylodidae					
	Hylodes meridionalis (Mertens, 1927)	H.mer	571	571	1
Leptodactylidae					
	Adenomera araucaria Kwet and Angulo, 2002	A.ara	621	1667	11
	Leptodactylus gracilis (Duméril and Bibron, 1840)	L.gra	312	621	260
	*Leptodactylus latrans**	L.lat	312	1796	1357
	Leptodactylus plaumanni Ahl, 1936	L.pla	571	1796	141
	Physalaemus lateristriga (Steindachner, 1864)	P.lat	712	712	33
	Physalaemus cuvieri Fitzinger, 1826	P.cuv	312	1425	231
	Physalaemus gracilis (Boulenger, 1883)	P.gra	929	1796	248
	Physalaemus nanus (Boulenger, 1888)	P.nan	322	1633	189
Microhylidae					
	Elachistocleis bicolor (Guérin-Méneville, 1838)	E.bic	322	1198	20
Odontophrynidae					
	Proceratophrys boiei (Wied-Neuwied, 1824)	P.boi	571	712	27
Phyllomedusidae					
	Phyllomedusa distincta Lutz, 1950	Phyl.dis	600	639	97

*We acknowledge that the taxonomic status of *L. latrans* was recently updated (Magalhães, F. D. M., Lyra, M. L., De Carvalho, T. R., Baldo, D., Brusquetti, F., Burella, P., ... & Garda, A. A. 2020. Taxonomic Review of South American Butter Frogs: Phylogeny, Geographic Patterns, and Species Delimitation in the Leptodactylus latrans Species Group (Anura: Leptodactylidae). Herpetological Monographs, 34(1), 131-177). And now, individuals here assigned to *L. latrans* could be either *L. paranaru* or *L. luctator*. Because proper indentification could only be archieved by inspecting individuals during the field work, we kept the name *L. latrans* as a conservative approach.

Table S1.4. Summary of generalized additive models used to assess the relationship of frog diversity (measured as Hill's numbers ^{q}D of order q = 0, 1, and 2) and abundance to (1) spatiotemporal variables, (2) temperature, and (3) residuals of spatiotemporal variables with the effect of mean monthly temperature removed, along the São Joaquim National Park and surrounding areas, southern Brazil.

Response	**Model type**	**Deviance explained (%)**	**Smooth terms**	**Edf**	**Ref edf**	**Chi.sq /F**	***p*-value**	**Fixed terms**	**Estimate**	**Standard error**	**z-value**	**p-value**
^{0}D	Spatiotemporal	68	s(elevation)	2.429	4	156.73	5.93e-06	Intercept	0.95	0.06	17.01	< 2e-16
			s(month)	6.574	8	400.83	< 2e-16					
			ti(month, elevation)	2.774	32	20.59	2.34e-05					
			s(pond id)	23.101	37	68.59	< 2e-16					
	Temperature	57.6	s(T_{mean})	3	4	391.45	< 2e-16	Intercept	0.99	0.06	16.44	< 2e-16
			s(pond id)	25.48	37	76.59	< 2e-16					
	Residuals (T_{mean})	25.3	s(elevation)	1.285	4	0.831	0.0745	Intercept	-0.19	0.05	-3.943	9.64e-05
			s(month)	6.586	8	13.959	< 2e-16					
			ti(month, elevation)	0.977	32	0.043	0.2189					
			s(pond id)	0.001	37	0	0.9455					
^{1}D	Spatiotemporal	61.3	s(elevation)	2.182	4	20.869	1.6e-06	Intercept	0.7	0.05	13.36	< 2e-16
			s(month)	5.996	8	34.913	< 2e-16					
			ti(month, elevation)	2.486	32	0.404	0.001170					
			s(pond id)	18.132	37	1.035	0.000323					
	Temperature	52.1	s(T_{mean})	2.908	4	66.672	< 2e-16	Intercept	0.73	0.06	13.14	< 2e-16
			s(pond id)	21.188	37	1.332	4.55e-05					
	Residuals (T_{mean})	23	s(elevation)	1.51	4	1.179	0.0423	Intercept	-0.16	0.04	-3.763	0.000195
			s(month)	6.308	8	12.31	< 2e-16					
			ti(month, elevation)	0.0003	32	0	0.612					
			s(pond id)	0.0007	37	0	0.8071					
^{2}D	Spatiotemporal	56.5	s(elevation)	2.052	4	14.955	1.41e-06	Intercept	0.58	0.05	11.14	< 2e-16
			s(month)	5.572	8	27.519	< 2e-16					
			ti(month, elevation)	2.256	32	0.304	0.00485					
			s(pond id)	14.849	37	0.704	0.00554					
	Temperature	47.9	s(T_{mean})	2.79	4	48.288	< 2e-16	Intercept	0.66	0.05	13	< 0.001
			s(pond id)	16.76	37	0.832	0.00292					
	Residuals (T_{mean})	21	s(elevation)	1.658	4	1.517	0.0231	Intercept	-0.16	0.04	-3.766	0.000193
			s(month)	6.146	8	10.574	< 2e-16					
			ti(month, elevation)	0.0005	32	0	0.6476					
			s(pond id)	0.002	37	0	0.4947					
Abundance	Spatiotemporal	66.4	s(elevation)	1.348	4	550.18	< 2e-16	Intercept	2.58	0.11	23.69	< 2e-16
			s(month)	6.305	8	579.44	< 2e-16					
			ti(month, elevation)	11.679	32	59.84	< 2e-16					
			s(pond id)	27.583	37	115.78	< 2e-16					
	Temperature	55.7	s(T_{mean})	3.089	4	596.85	< 2e-16	Intercept	2.699	0.11	24.62	< 2e-16
			s(pond id)	26.438	37	89.28	< 2e-16					
	Residuals (T_{mean})	27.3	s(elevation)	1.118	4	2.071	0.00303	Intercept	-0.35	0.04	-8.08	1.01e-14
			s(month)	6.559	8	10.942	< 2e-16					
			ti(month, elevation)	9.088	32	0.74	0.00163					
			s(pond id)	0.0006	37	0	0.96806					

Table S1.5. Summary of the spatiotemporal and temperture generalized additive models with and without pond's coordinates to account for any spatial autocorrelation including frog diversity (measured as Hill's numbers ^{q}D of order $q = 0$, 1, and 2) and abundance as response variables. Models are ranked by ΔAIC, with values < 2 indicating equally well supported.

Response	**Model type**	**Deviance explained (%)**	**df**	**AIC**	**ΔAIC**
^{0}D	Spatiotemporal	68	38.82	1404.784	0
	Spatiotemporal + s(x, y)	68.7	47.61	1414.602	9.818
	Temperature	57.6	31.72	1505.287	0
	Temperature + s(x, y)	57.6	31.66	1505.665	0.378
^{1}D	Spatiotemporal	61.3	34.56	1177.459	0
	Spatiotemporal + s(x, y)	61.3	36.12	1180.44	2.981
	Temperature	52.1	28.54	1236.319	0
	Temperature + s(x, y)	52.1	28.77	1236.663	0.344
^{2}D	Spatiotemporal	56.5	31.1	1154.327	0
	Spatiotemporal + s(x, y)	56.5	32.61	1157.209	2.882
	Temperature	47.9	24.44	1195.145	0
	Temperature + s(x, y)	47.9	24.64	1195.571	0.426
Abundance	Spatiotemporal	66.4	53.38	2881.291	0.207
	Spatiotemporal + s(x, y)	66.3	52.73	2281.084	0
	Temperature	59.2	35.44	2931.586	1.136
	Temperature + s(x, y)	59.2	34.96	2930.224	0

Appendix S2. Additional figures

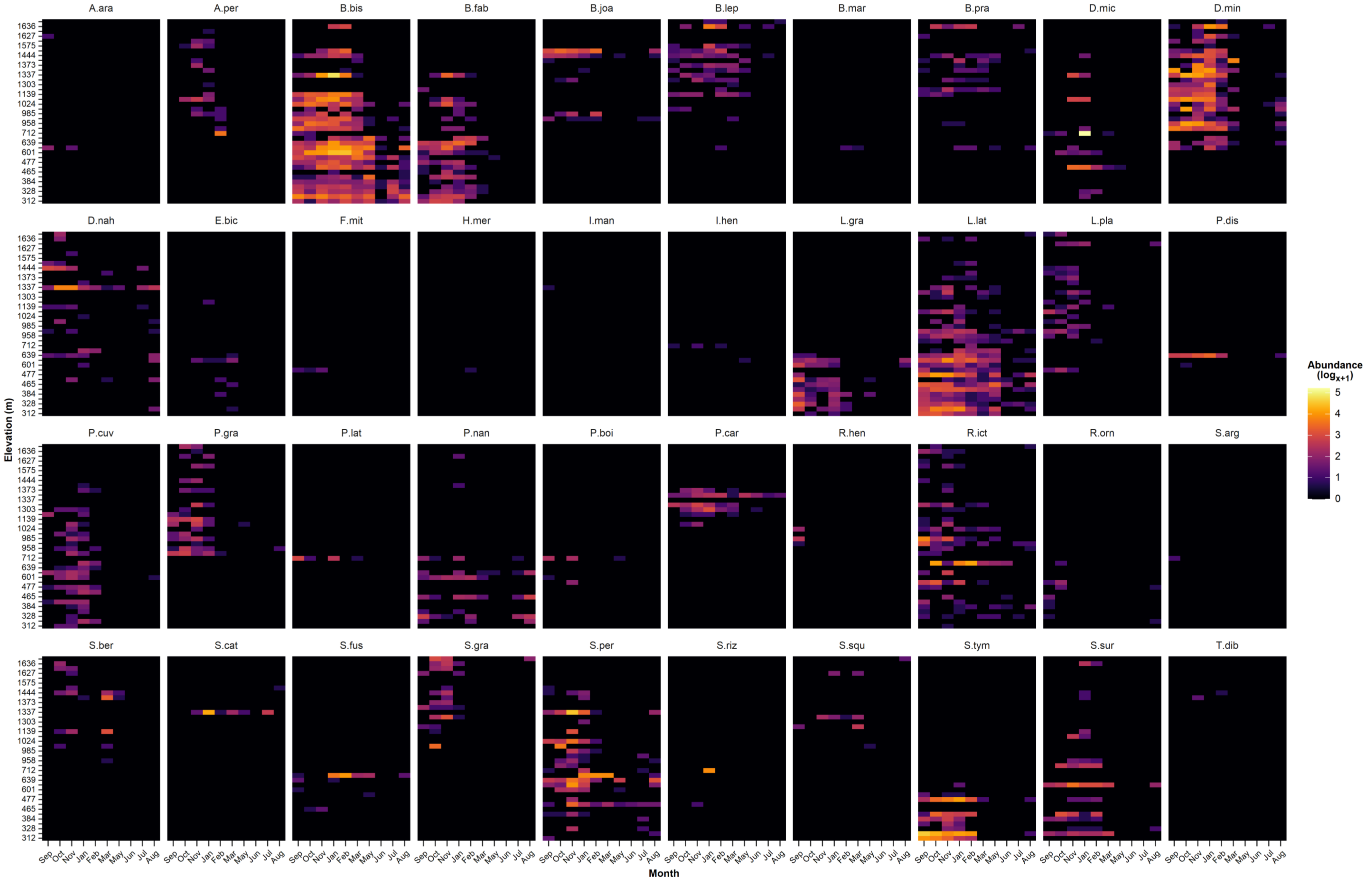

Figure S2.1. Abundance ($\log_{x+1}$ transformed for better visualization) per sampled month (September 2017 to August 2018) per elevation (38 surveyed ponds) of the 40 frog species found at SJNP and surrounds, Santa Catarina, Brazil. Species abbreviation code follows Table S1.3.

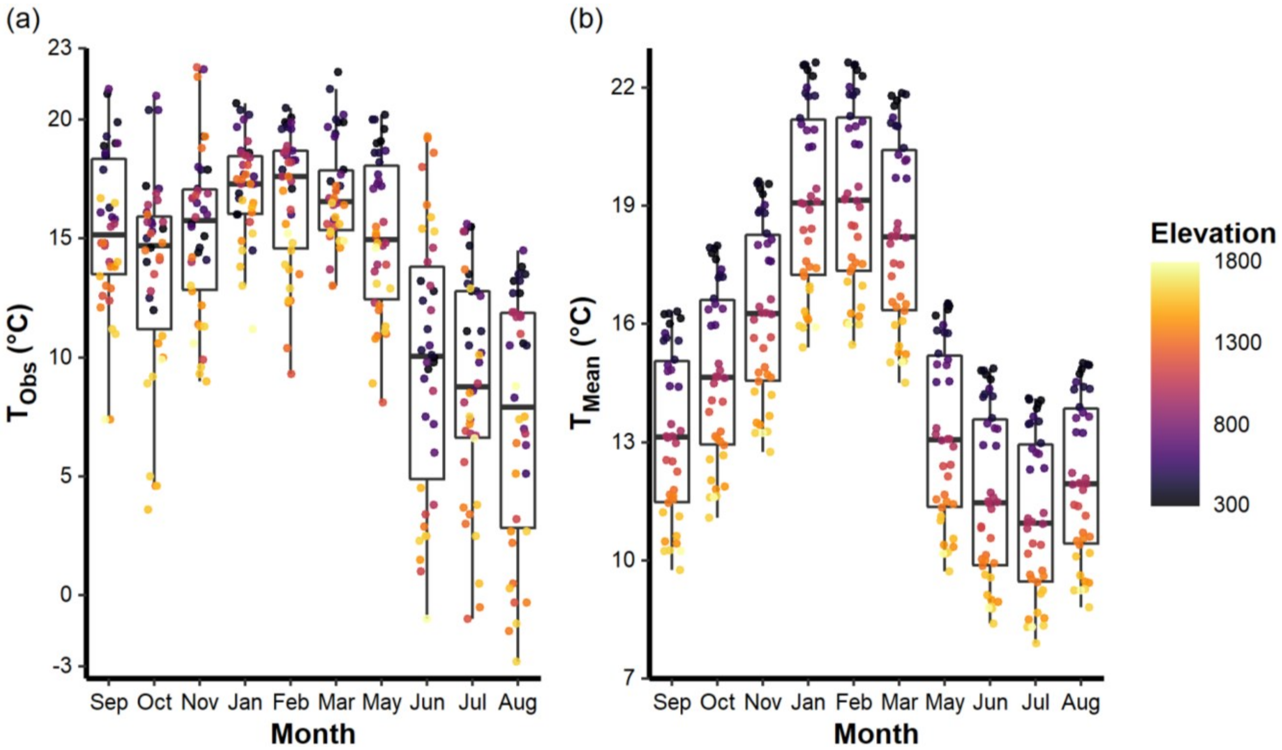

Figure S2.2. Temperature variation between September 2017 and August 2018 at the 38 surveyed ponds along the elevational gradient located at SJNP and surrounds, Santa Catarina, Brazil. (a) Mean temperature observed during surveys (T_{Obs}); (b) Estimated mean monthly temperature (T_{mean}) over pond's elevational bands (see main text for how values were calculated). Note that plots have different scales in *y* axis. Thick boxplot line represents the median of each month and colours indicate ponds' elevation.

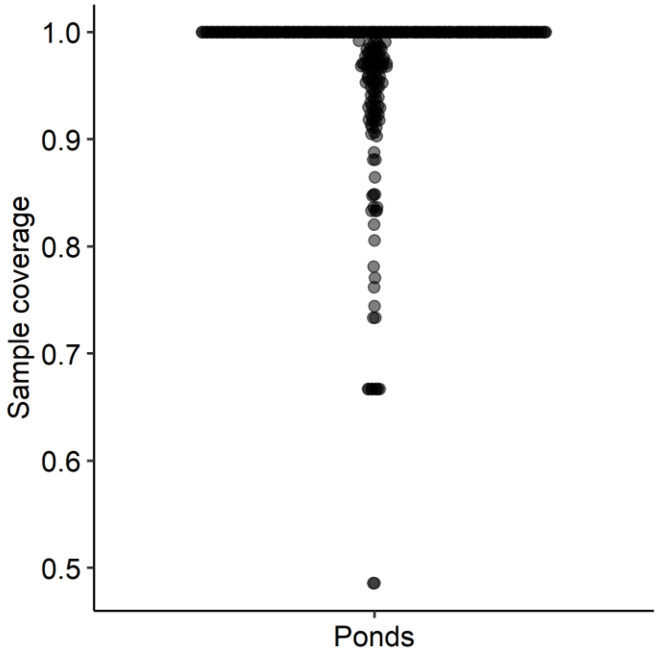

Figure S2.3. Sample coverage values obtained for the 380 sampled assemblages (i.e., 38 ponds x 10 months) at SJNP and surrounds, Santa Catarina, Brazil.

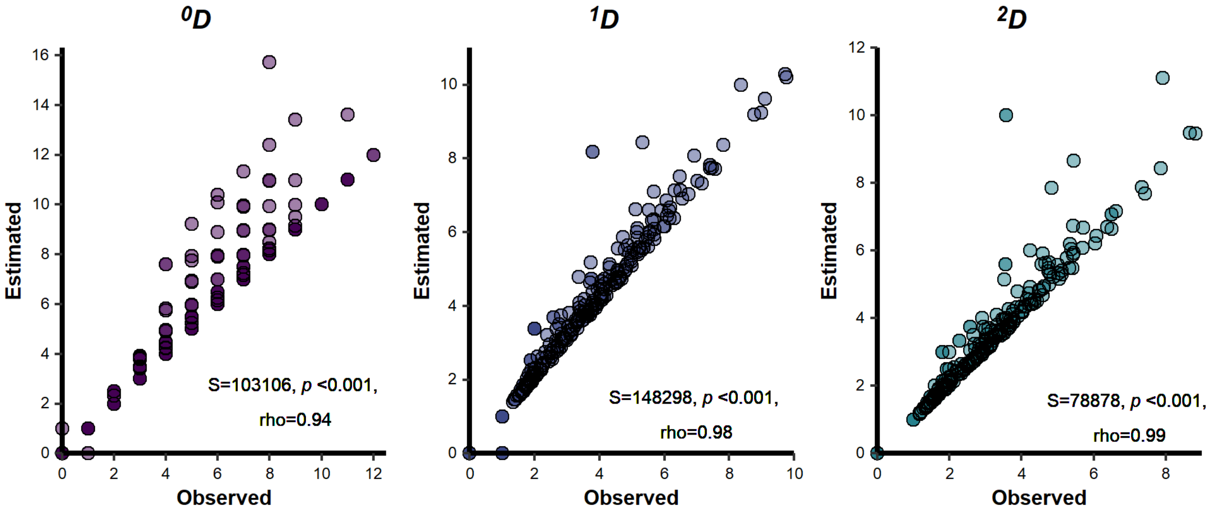

Figure S2.4. Spearman's rank-order correlation and respective p-values between observed and estimated frog diversity (i.e., ^0D, ^1D, and ^2D) at SJNP and surrounds, Santa Catarina, Brazil. Points represent the 380 sampled frog assemblages (i.e., 38 ponds x 10 months).

4 CONCLUSÃO GERAL

Os ambientes montanhosos abrigam elevada biodiversidade, das quais muitas são endêmicas e apresentam adaptações para sobreviver às condições encontradas nessas áreas. Entretanto, cada vez mais esses ambientes e as espécies que neles vivem têm sido ameaçadas pela perda de suas áreas naturais, mas também com o avanço das mudanças climáticas. Dessa forma, entender os processos que levam à distribuição da diversidade ao longo desses gradientes elevacionais se faz imprescindível para a conservação desses ambientes. Essa tese apresenta contribuições substanciais para um melhor entendimento acerca dos mecanismos envolvidos nos padrões de distribuição da diversidade ao longo de gradientes elevacionais. Combinando dados coletados em escala local e levando em consideração os possíveis efeitos da sazonalidade, foi possível realizar a primeira análise espaço-temporal da diversidade de anfíbios anuros ao longo de um extenso gradiente elevacional Neotropical. Os padrões aqui encontrados são consistentes com a ideia de que os diferentes componentes da diversidade de anuros são influenciados por mecanismos atrelados a filtros ambientais existentes ao longo dos gradientes elevacionais. Uma vez que a composição das assembleias das áreas baixas se mostrou diferente das áreas mais elevadas, ressaltamos a importância de toda a região montanhosa para a manutenção da diversidade em escala regional. A temperatura se mostrou um importante preditor dos padrões espaço-temporais da diversidade de anuros. O aumento da temperatura a nível global decorrente das mudanças climáticas tem afetado o limite de distribuição de múltiplas espécies. Logo, entender os diferentes processos por trás dos componentes da biodiversidade é de extrema importância para sua conservação. Assim, os resultados desse estudo podem ser usados como base para futuros estudos que se proponham a avaliar o impacto das mudanças climáticas nas espécies de anuros ao longo da Mata Atlântica, bem como para o desenvolvimento de estratégias de conservação mais efetivas em seus ambientes montanhosos.

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