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**EFEITOS DO HUMAN FOOTPRINT, ESPÉCIES
INVASORAS E DE DOENÇAS EMERGENTES EM
PADRÕES DE DIVERSIDADE DE ANFÍBIOS
NEOTROPICAIS**

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NEOTROPICAIS**

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Resumo geral

Os anfíbios são um dos principais grupos de vertebrados ameaçados globalmente, sofrendo declínios constantes. Diversas as ameaças são responsáveis por esses declínios, tais como as mudanças climáticas, fragmentação do habitat e conversão de áreas naturais, além de agentes patogênicos e espécies invasoras. Anfíbios são afetados por essas ameaças devido a aspectos de sua história de vida, tais como dependência de ambiente aquático, sua fisiologia e sensibilidade à variação de temperaturas. Apesar do conhecimento sobre esses impactos, ainda é incerto de que maneira eles estão atuando em conjunto para o declínio dos anfíbios e como afetam as diferentes facetas da diversidade (taxonômica, funcional e filogenética) na região neotropical. Assim, essa tese teve como objetivos (Capítulo 1) investigar como mudanças climáticas globais em conjunto com espécies invasoras (nesse caso a *Lithobates catesbeianus* - *Lc*) (Shaw, 1802) (Anura: Ranidae) e o fungo quitrídio (*Batrachochytrium dendrobatidis* - *Bd*) (Berger, 1998) (Fungi, Chytridiomycota, Rhizophydiales), causador da quitridiomicose, afetam a distribuição de anuros no neotrópico. Além disso, (Capítulo 2) buscamos entender de que maneira as ameaças antrópicas afetam as diferentes facetas da diversidade de anfíbios na região neotropical e de que maneira elas se relacionam com a distribuição de *Bd* e *Lc*. No primeiro capítulo geramos modelos de distribuição potencial para *Bd* e *Lc* e para 46 espécies de anuros neotropicais para os cenários atuais e para o futuro (2100). Além disso, testamos a sobreposição de nicho climático e também dos mapas de adequabilidade gerados e os comparamos. A distribuição de espécies nativas de anuros tende a diminuir nos próximos anos devido às mudanças climáticas, enquanto a da espécie invasora rã-touro e o *Batrachochytrium dendrobatidis* (*Bd*), irão aumentar nos próximos anos, se sobrepondo com as espécies nativas. Assim, haverá um efeito sinérgico dessas ameaças, acentuando ainda mais o seu declínio. No segundo capítulo testamos como as variáveis

de uso do solo e densidade populacional humana (usadas para a criação do índice *Human Footprint - HF*), afetam diferentes facetas da diversidade e como essa diversidade está relacionada com a distribuição potencial de *Bd* e *Lc*. Para isso, coletamos as informações das espécies a partir dos dados da IUCN e a partir daí calculamos a riqueza (diversidade taxonômica), diversidade funcional e filogenética de espécies. Coletamos também as informações das variáveis antrópicas a partir de bases de dados e geramos modelos de distribuição atual para *Bd* e *Lc* (mesmos modelos do capítulo 1). Verificamos que as facetas da diversidade são em geral negativamente relacionadas a com as variáveis antrópicas na maior parte da região neotropical. Além disso, a maior parte da diversidade está localizada em regiões onde o *Bd* é presente. Somado a isso, tanto o *Bd*, quanto a *Lc* tendem a ocorrer em regiões em que as variáveis de uso do solo como monoculturas e pastagens são maiores. Assim, temos além da fragmentação de ambientes naturais do anuros neotropicais, a influencia negativa das espécies invasoras. Essas ameaças podem levar a extinção não somente de espécies, mas para a perda de atributos funcionais e linhagens inteiras. Dessa maneira, é necessário considerar essas ameaças e elaborar políticas e planos de conservação que levem em consideração a ação delas em conjunto, evitando assim homogeneização da diversidade e a manutenção das áreas de ocorrência das espécies de anuros neotropicais.

General abstract

Amphibians are one of the main groups of globally threatened vertebrates, suffering constant declines. Several threats are responsible for these declines, such as climate change, habitat fragmentation and conversion of natural areas, as well as pathogens and invasive species. Amphibians are affected by these threats due to aspects of their life history, such as dependence on the aquatic environment, their physiology and sensitivity to temperature variations. Despite the knowledge about these impacts, it is still uncertain how they are acting together for the decline of amphibians and how they affect the different facets of diversity (taxonomic, functional and phylogenetic) in the Neotropics. Thus, this thesis aimed (Chapter 1) to investigate how global climate change in conjunction with invasive species (in this case *Lithobates catesbeianus* - *Lc*) (Shaw, 1802) (Anura: Ranidae) and the chytrid fungus (*Batrachochytrium dendrobatidis* - *Bd*) (Berger, 1998) (Fungi, Chytridiomycota, Rhizophydiales), which causes chytridiomycosis, affect the distribution of anurans in the Neotropics. In addition, (Chapter 2) we seek to understand how anthropic threats affect the different facets of amphibian diversity in the region neotropical and how they relate to the distribution of *Bd* and *Lc*. In the first chapter we generate potential distribution models for *Bd* and *Lc* and for 46 Neotropical anuran species for the current and future (2100) scenarios. In addition, we tested the overlapping of climatic niches and also the generated suitability maps and compared them. The distribution of native anuran species tends to decrease in the coming years due to climate change, while that of the invasive bullfrog species and *Batrachochytrium dendrobatidis* (*Bd*) will increase in the coming years, overlapping with native species. Thus, there will be a synergistic effect of these threats, further accentuating their decline. In the second chapter, we tested how the variables of land use and human population density (used to create the *Human Footprint Index* - *HF*) affect different facets

of diversity and how this diversity is related to the potential distribution of *Bd* and *Lc*. For this, we collected species information from IUCN data and from there we calculated the richness (taxonomic diversity), functional and phylogenetic diversity of species. We also collected information on anthropogenic variables from databases and generated current distribution models for *Bd* and *Lc* (same models as in Chapter 1). We found that facets of diversity are generally negatively related to anthropic variables in most of the Neotropical region. Furthermore, most of the diversity is located in regions where *Bd* is present. Added to this, both *Bd* and *Lc* tend to occur in regions where land use variables such as monocultures and pastures are greater. Thus, in addition to the fragmentation of natural environments of Neotropical anurans, we have the negative influence of invasive species. These threats can lead to the extinction not only of species, but to the loss of functional attributes and entire lineages. Thus, it is necessary to consider these threats and develop policies and conservation plans that take into account their action together, thus avoiding the homogenization of diversity and the maintenance of areas of occurrence of Neotropical anuran species.

Introdução geral

A perda da biodiversidade é um dos principais problemas ambientais da atualidade, ameaçando serviços ecossistêmicos e o bem estar humano (Ceballos et al. 2010, 2017, Barnosky et al. 2011, Cardinale et al. 2012). Essa perda da diversidade biológica tem sido causada pelo homem, direta ou indiretamente (Dirzo et al. 2014, Young et al. 2016) e envolve perda e fragmentação de hábitat, superexploração, introdução de espécies exóticas, mudanças climáticas e poluição (Young et al. 2016). Atualmente estamos vivendo a sexta extinção em massa, afetando de forma direta e desigual diversas espécies (e.g. anfíbios; Hof et al. 2011, Pimm et al. 2014, Pincheira-Donoso et al. 2022), em regiões específicas do mundo (e.g. neotrópico; Ceballos et al. 2017; Urban 2015).

A região neotropical possui altos índices de desmatamento, além de diversas espécies ameaçadas (IUNC 2022), aumentando a probabilidade de extinções e acentuando o declínio da diversidade (Betts et al. 2017, de Oliveira Roque et al. 2018). Anfíbios são um dos grupos mais diversos e ameaçados na região neotropical, com taxas de ameaças de extinção maiores do que outros vertebrados (Pimm et al. 2014, IUNC 2022, Pincheira-Donoso et al. 2022). Além disso, eles possuem restrições no uso do tipo de habitat, uma vez que grande parte se desenvolve na água, se reproduzem e habitam preferencialmente em ambientes úmidos (Jenkins et al. 2013). Assim, anfíbios possuem diversas ameaças como a fragmentação do habitat (Becker et al. 2007), alterações das paisagens naturais (Nowakowski et al. 2018), agentes patogênicos e espécies invasoras (Bellard et al. 2016, Doherty et al. 2016), poluição (Schiesari et al. 2007) e mudanças climáticas (Daufresne et al. 2009, Li et al. 2013).

Essas ameaças podem afetar os anfíbios de várias maneiras. Por exemplo, as mudanças no uso do solo podem alterar o seu habitat reduzindo áreas adequadas para a sobrevivência e persistência (Nowakowski et al. 2018), influenciando dispersão, história

de vida e causando a extinção de espécies (Mac Nally et al. 2009). Isso se deve às limitações fisiológicas e de história de vida que os anfíbios possuem (Cushman 2006, Barrett and Guyer 2008). Em escalas mais amplas, essas alterações no habitat podem reduzir a riqueza e abundância (Nowakowski et al. 2018).

Outra importante ameaça são as mudanças climáticas que afetam a distribuição de vários grupos de espécies, em especial os anfíbios (Schivo et al. 2019). Por exemplo, com as mudanças climáticas as espécies devem buscar locais com maior adequabilidade climática para sua sobrevivência e persistência. No entanto, devido aos limites de dispersão dos anfíbios, somados às alterações climáticas, é esperado que a distribuição dessas espécies diminuirá nas próximas décadas (Lawler et al. 2010).

Outras ameaças à diversidade de anfíbios são espécies invasoras e doenças emergentes, tais como a quitridiomicose (Bellard et al. 2016, Doherty et al. 2016). A rã-touro (*Lithobates catesbeianus*) por exemplo, é uma espécie invasora que compete e preda diversas espécies de anfíbios (Ficetola et al. 2007), promovendo declínios globais (Kraus 2015). Em conjunto, a quitridiomicose, causada pelo fungo *Batrachochytrium dendrobatidis* (*Bd*) afeta diversas espécies de anuros, causando declínio em escala global (O'Hanlon et al., 2018; Rosenblum et al., 2010). Além disso, a rã-touro pode ser infectada pelo *Bd*, mas não apresentar sintomas da infecção, atuando como potencial vetores, atuando de maneira sinérgica, aumentando ainda mais o declínio de anfíbios pelo mundo (Yap et al., 2018).

Dessa forma, as espécies de anfíbios são impactadas por diversas ameaças. No entanto, essas ameaças não atuam de maneira isolada (Carrasco et al. 2021). Além disso, crescentes impactos estão sendo destacados na região neotropical, comprometendo diversas espécies e aumentando o declínio de anfíbios (Betts et al., 2017; De Oliveira Roque et al., 2018). Com base nessas informações, investigamos como múltiplas ameaças

têm afetado anfíbios na região neotropical. No Capítulo 1, verificamos a influência das mudanças climáticas globais na distribuição de anuros neotropicais. Além disso, testamos o grau de sobreposição do nicho climático da rã-touro e *Bd* em relação ao de espécies nativas, prevendo o efeito sinérgico das mudanças climáticas, espécies invasoras e quitridiomicose. No capítulo 2 como as múltiplas facetas da diversidade (taxonômica, funcional e filogenética) estão relacionadas com variáveis antrópicas ligadas a mudanças no uso do solo e densidade populacional humana. Além disso, buscamos entender de que forma a distribuição potencial atual de *Bd* e *Lc* se relaciona com a diversidade de sapos neotropicais e essas variáveis antrópicas abordadas.

Chapter 1

Influence of global climate change, invasive species and emerging diseases on native Neotropical frogs

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Abstract

Amphibians are among the most threatened group because of their significant vulnerability to environmental changes, especially climate change that is causing distributional changes, fitness decreases, and species extinction. Additionally, invasive species can be competitors and predators of other amphibian species. Thus, it is not known how climate change and invasive species may impact the distribution of Neotropical native frog species. Here, we tested the synergistic effect of climate change, overlap with invasive species, and emerging diseases for Neotropical amphibians. We collected occurrence data for 46 native frog species and *Bd* and *Lc*. Then, we applied environmental niche models to predict the potential distribution in the present and for the year 2100. We calculated niche overlaps of *Lc* and *Bd* and native frogs for both scenarios. We found that both *Bd* and *Lc* have a high niche overlap and niche suitability overlap with native neotropical frog species. We also observed that native species tend to decrease

their distribution and *Lc* and *Bd* tend to increase with global climate changes. These results suggest that the combined effect of climate change and overlap between invasive species and chytrid fungus may impact the distribution of Neotropical native species. Thus, conservation policies need a more holistic view, considering the synergistic effects of climate change, emerging diseases, and invasive species.

Keywords: amphibians, chytridiomycosis, American bullfrog, niche overlap, suitability overlap.

Introduction

Biodiversity loss is an emerging problem, affecting species globally and causing range shifts (Pereira et al. 2012). One of the main threats to biodiversity are the introduction of invasive species, climate change, and emerging diseases (Tylianakis et al. 2008, Young et al. 2016). Amphibians are among the most threatened species, with rapid population decline (Pimm et al. 2014, Ceballos et al. 2020). One of the main threats to amphibians is climate change, which can change geographic distribution (Daufresne et al. 2009, Li et al. 2013). A change in the range of several species is expected (Schivo et al. 2019), while others are expected to disperse to favorable regions (Araújo et al. 2006, Lawler et al. 2010). However, for species with low dispersal rates, a decrease in their distribution in climate scenarios is expected until 2071. (Lawler et al. 2010).

Invasive species and emerging diseases also contribute to amphibian declines (Bellard et al. 2016, Doherty et al. 2016). The American bullfrog (*Lithobates catesbeianus*) has been introduced in several parts of the world (Ficetola et al. 2007), causing amphibian decline worldwide (Kraus 2008). The fungus *Batrachochytrium dendrobatidis* (*Bd*), may also be related to this decline (Rosenblum et al. 2010), because

it has a wide distribution and infects several amphibians (O’Hanlon et al., 2018). Interestingly, bullfrogs are commonly infected by this fungus, and while they do not develop symptoms, they can still act as vectors (Daszak et al., 2004). Therefore, the presence of *Lc* and *Bd* may represent additive effects on amphibian communities (Yap et al., 2018).

The Neotropics has high climatic suitability for invasive species while also harboring biodiversity hotspots (e.g., Cerrado, Atlantic Forest; Mittermeier et al., 2011), with a high richness of endangered species. This scenario suggests that amphibian diversity in the region can be highly impacted by climate change (Tylianakis et al. 2008, Gallardo et al. 2015), and infection by the chytrid fungus (Grant et al., 2016). However, little or nothing is known about the joint effect of climate change and invasive species on the distribution of Neotropical frog species.

Here, we asked whether: i) the climatic niche of the invasive species and *Lithobates catesbeianus* (*Lc*) will overlap in the present and future with the fungus *Batrachochytrium dendrobatidis* (*Bd*) in the Neotropics; ii) The climatic niche of native species will overlap with that of *Bd* and *Lc*. We expect that regions with climate suitability for *Bd* and *Lc* will overlap with that for native species currently and in the future. This is due to the high dispersal and colonization abilities of *Lc* (Giovanelli et al. 2008, Nori et al. 2011). Finally, we expect that areas with climatic suitability for native species will be reduced (Tylianakis et al. 2008, Gallardo et al. 2015).

Methods

Target species and occurrence database

We compiled occurrence data for 46 native frog species and *Lc* from the Global Biodiversity Information Facility - GBIF database (<http://www.gbif.org>, accessed August

2020 – October 2021 – DOI: <https://doi.org/10.15468/dl.a9nj77>). All 46 frog species had at least one record of infection by *Bd*. *Bd* occurrence data was provided by experts (courtesy of researchers Deanna H. Olson and Kathryn L. Ronnenberg, accessed July 2020), collected around the world between 1835 and 2014. We cleaned data to avoid possible biases by removing i) duplicated records; ii) records with missing coordinates; iii) records falling on oceans using the package *CoordinateCleaner* (Zizka et al. 2019). Additionally, we iv) filtered occurrence records from a minimum distance of 10 km to minimize sampling bias using the package *spThin* (Aiello-Lammens et al., 2015).

Climate data

We downloaded data for 19 climatic variables and elevation (Supplementary Table S1) in *WorldClim* version 2.1 (<https://www.worldclim.org/>; accessed August 2020, (Fick and Hijmans 2017), with a spatial resolution of 5 arc-minutes (~18.5 km at the equator) for the World and Neotropics for the present (1970 –2000) and the most pessimistic future scenario (CMIP6 – SSP8.5 for 2081–2100).

Ecological niche modeling

Firstly, we performed a principal component analysis (PCA) for the 19 bioclimatic and altitude variables. We used global (for *Lc* and *Bd*) and Neotropical extensions (native species of frogs) to develop models niche suitability. We retained the first six components (96% of variation) for the global models used in *Lc* and *Bd*. For the neotropical extension models for native species, we also retained the first six principal components (92% of variation). The 19 bioclimatic and altitude variables were first standardized with mean and variance equal to zero, and after that a PCA was generated, using the axes as new predictive variables in our global distribution (for *Lc* and *Bd*) and neotropical models (native species of frogs). We used as an accessible area in our models for our native

species the morphoclimatic domains according to the criteria of biogeographic regionalization of the Neotropical region (Löwenberg-Neto 2014, Morrone 2014; Supplementary Table S2). Thus, we performed different models with different accessible areas for each frog species. For example, for species with restricted occurrence in the Atlantic Forest or the Cerrado, niche models were generated based on these specific morphoclimatic domains. We generated the distribution models of the species using the following modeling methods: general linear models (GLM; (Guisan et al. 2002), generalized additive model (GAM; (Guisan et al. 2002), boosted regression tree (BRT; Hijmans et al., 2017), maxent (MXS; (Phillips et al. 2006, Phillips 2017), Gaussian Process (GAU; (Weir and Pettitt 2000), random forest (RDF; (Cutler et al. 2007), maximum likelihood (MLK; (Royle et al. 2012) and support vector machine (SVM; Liu et al., 2010).

We generated models for *Bd* and *Lc* for the whole world and then cropped them to the Neotropics for comparison with the native frog species. All niche models were generated in the *ENMTML* package version 1.0.0 (de Andrade et al. 2020). We estimated the maximum True Skill Statistic (TSS - (Allouche et al. 2006), which ranges from -1 to 1, with models close to 1 considered excellent models, while negative models or close to zero are bad ones. Finally, we use an ensemble (Araújo and New 2007) to calculate the average of the best models for each species (Supplementary Table S3). We describe an ODMAP (Overview, Data, Model, Evaluation, and Prediction) reporting protocol. This protocol provides a standardized way to communicate SDM results and outputs, describing objectives, model assumptions, scaling issues, data sources, model workflows, model predictions, and uncertainties (Supplementary Table S4).

Niche Analysis

We performed a PCA (PCA-env) calibrated for the entire environmental space to measure the niche overlap (Strubbe et al. 2013). Climatic niche overlap follows: i) calculating occurrence density and environmental factors using multivariate methods, ii) measurement of niche overlap and iii) niche similarity analysis. We use *Schoener's D* index to evaluate niche overlap between *Lc*, *Bd*, and native species (Warren et al. 2008). We also measured the niche overlap between *Lc* and *Bd* suitability maps *and between these and native species* for the current and future scenarios. We performed a beta regression in the *betareg* package version 3.3-3 (Zeileis et al. 2016). This analysis was performed using the *ENMTools* package version 1.0.5 (Warren et al. 2010). We also used linear models to compare the suitable area for native species in the current and future scenarios (Zuur et al. 2010).

Phylogenetic signal

We calculated the phylogenetic signal for the present and future scenarios overlap between *Lc* and *Bd* and native species. We also calculated the phylogenetic signal for the difference in a suitable area in the present and future scenario for the native species. To calculate the phylogenetic signal, we pruned the species to which we have data from the consensus topology of Jetz & Pyron, 2018. Then, we estimated the phylogenetic signal for suitability and difference suitability (future – current) overlap using a Blomberg's *K* statistic (Blomberg et al. 2003) in the *phytools* package (Ives et al. 2007, Revell 2012).

Results

All models had good to excellent performances for both invasive and native species (*Lc*: TSS = 0.95; *Bd*: TSS = 0.96; statistics for 34 native species: TSS max = 1, TSS min = 0.90, average TSS = 0.94, TSS SD = 0.02, statistics for the remaining 12

species: TSS max = 0.88, TSS min = 0.76, mean TSS = 0.84, TSS SD = 0.03).

There was a large overlap in the suitable area between *Bd* and *Lc* for the present ($D = 0.45$), which increased in the future ($D = 0.62$). There was a decrease in the suitable area overlap between *Bd* and native species in the present ($n = 46$, mean = 0.45, SD = 0.07) and the future ($n = 46$; mean $D = 0.40$; SD = 0.07, $Z = -3.131$; $P = 0.002$, Fig 1a). There was an increase in the future suitable area for *Bd* (suitable area at present = 20,434,331 Km²; in the future = 21,390,895 Km²). Suitability overlap between *Lc* and native species decreased between present models ($n = 46$, mean = 0.44, SD = 0.08) to future scenario models ($n = 46$; mean $D = 0.41$; SD = 0.07; $Z = -1.954$; $p = 0.05$, Fig. 1b). This same increase occurred between the present and future for *Lc* (suitable area in the present = 8,955,917 Km²; in the future scenario = 13,199,543 Km²). Additionally, suitable area (Km²) for native species decreased from the present to the future ($t = -2.098$; $P = 0.03$, Fig 2).

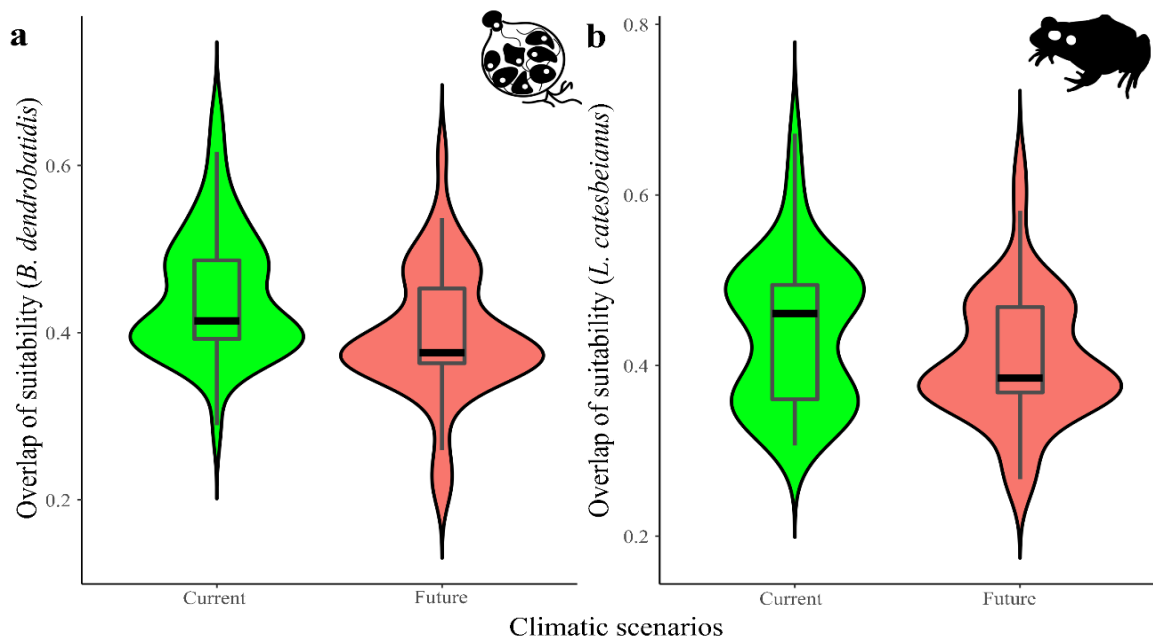


Figure 1 – Overlap in the suitable area between native species and *Bd* (a) and *Lc* (b) for the present and future. In all violin plots, gray boxes span the first quartile to the third quartile; black lines in gray boxes indicate the median; and the widths contained in a violin plot indicate the kernel density. All silhouettes were obtained from phylopic (<<http://phylopic.org/>>).

The first two PCA-env axes retained 71.07% of the variation in climatic variables (PC1 = 51.31%, PC2 = 19.76%). We found a high niche overlap between *Bd* and *Lc* ($D = 0.52$). However, there was a low niche overlap between *Bd* and native species ($n = 46$; mean $D = 0.18$; $SD = 0.12$; range = 0.03–0.64, Fig 3), but only a moderate niche overlap between *Lc* and native species ($n = 46$; mean $D = 0.24$; $SD = 0.13$; range = 0.05–0.66, Fig 4). However, some species had a high niche overlap with *Lc*, such as *Boana pulchella* ($D = 0.41$), *Leptodactylus wagneri* ($D = 0.43$), *Scinax fuscovarius* ($D = 0.46$), *Dendropsophus minutus* ($D = 0.55$) and *Leptodactylus latrans* ($D = 0.66$).

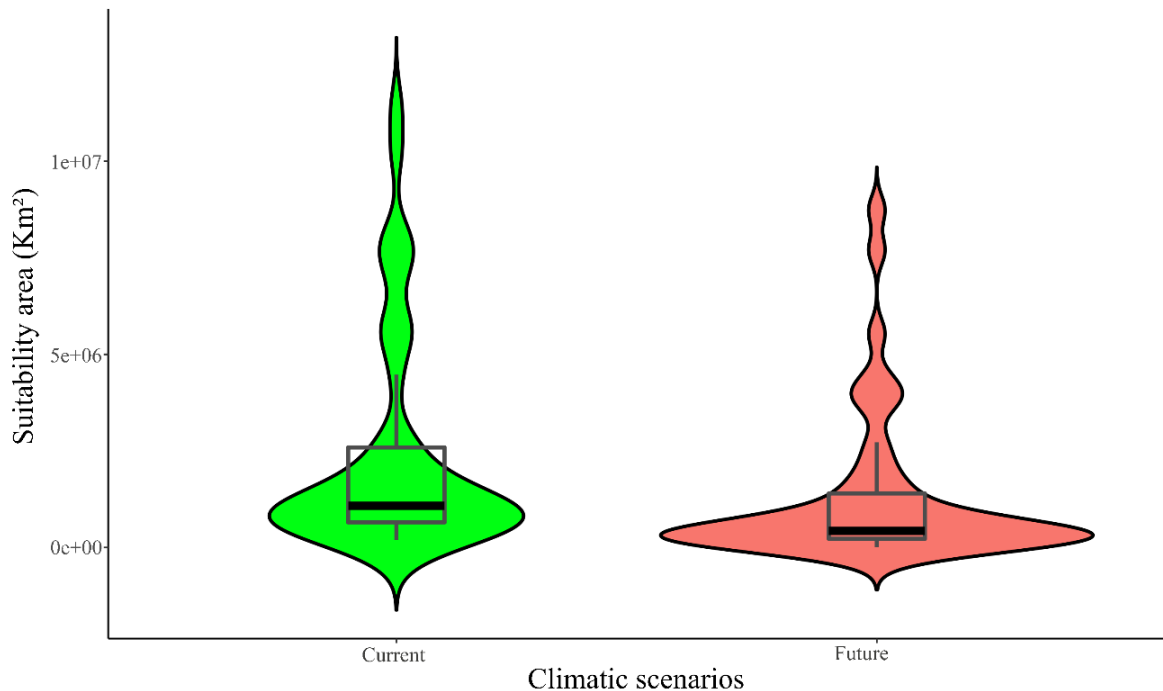


Figure 2 – Comparison of areas of suitability of native frog species for present and future models. In all violin plots, gray boxes span the first quartile to the third quartile; black lines in gray boxes indicate the median; and the widths contained in a violin plot indicate the kernel density.

We found phylogenetic signal neither for the suitability overlap between *Lc* and native species for the present ($K = 0.257$, $P = 0.3$) nor the future ($K = 0.216$, $P = 0.5$) and between *Bd* and native species for the present ($K = 0.2892$, $P = 0.3$) or the future ($K = 0.186$, $P = 0.6$). However, the difference in suitable area (future-present) of native species had a weak phylogenetic signal ($K = 0.526$, $P = 0.05$, Fig 5). Interestingly, some species

seem to have benefited from climate change, while most tend to decrease their areas in future scenarios (Fig. 5).

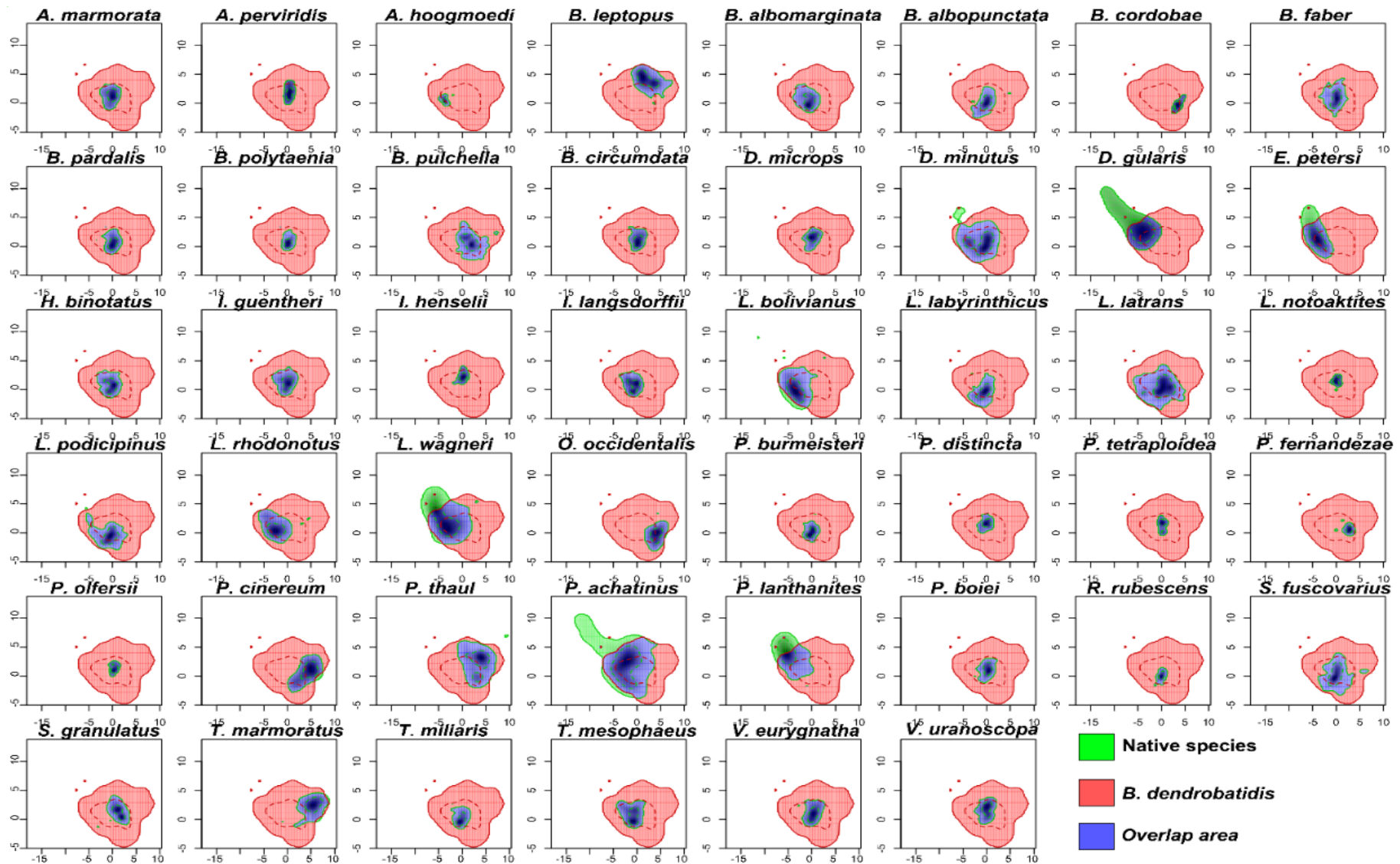


Figure 3 - Environmental niche overlap between Bd and native anuran species. Green colors represent niche occupation for native Neotropical frog species. Pink colors indicate occupation of the niche for *B. dendrobatidis*. Purple colors indicate niche overlap between Neotropical frog species and *B. dendrobatidis*.

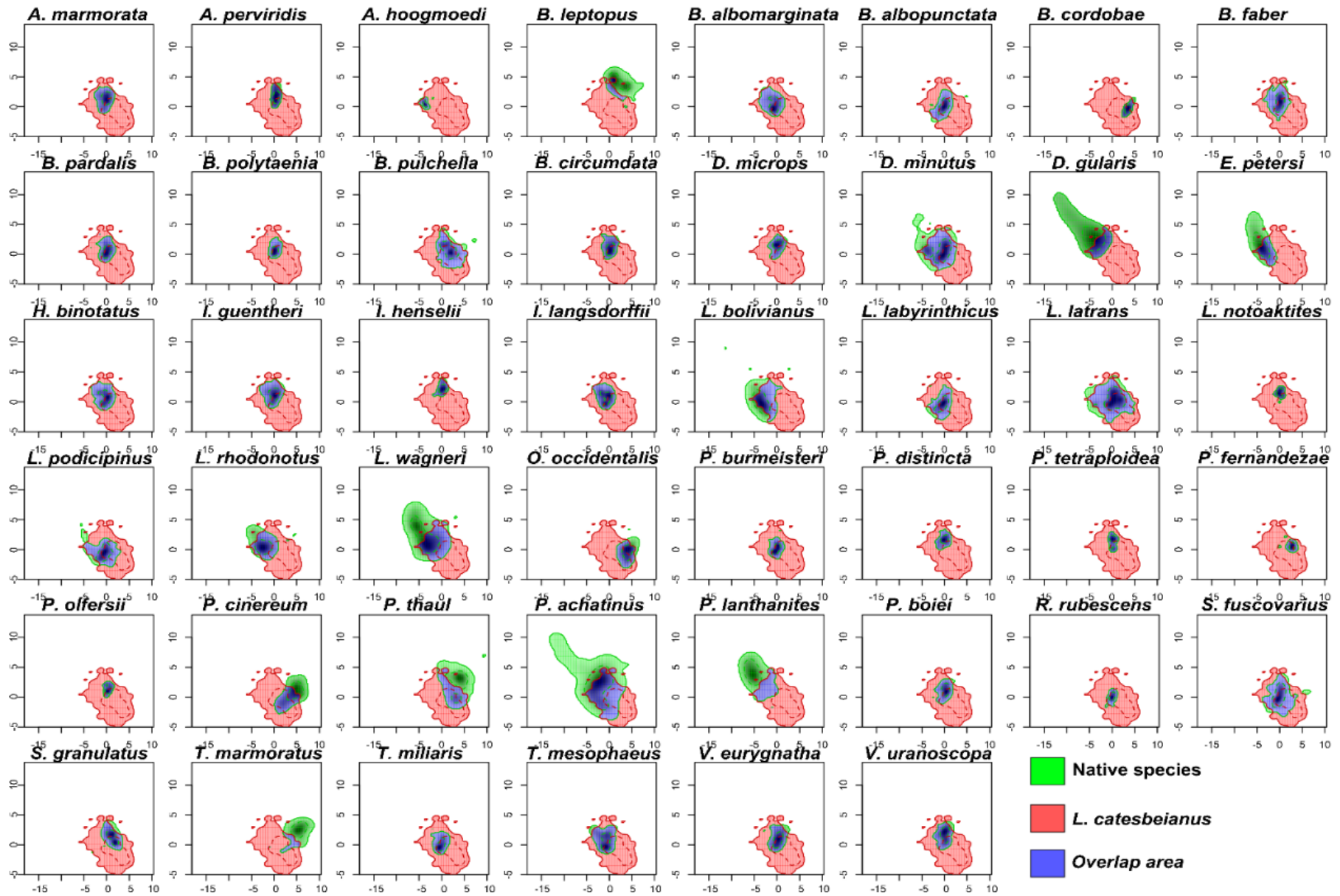


Figure 4 - Environmental niche overlap between *Lc* and neotropical native species. Green colors represent niche occupation for native Neotropical frog species. Pink colors indicate occupation of the niche for *B. dendrobatidis*. Purple colors indicate niche overlap between Neotropical frog species and *B. dendrobatidis*.

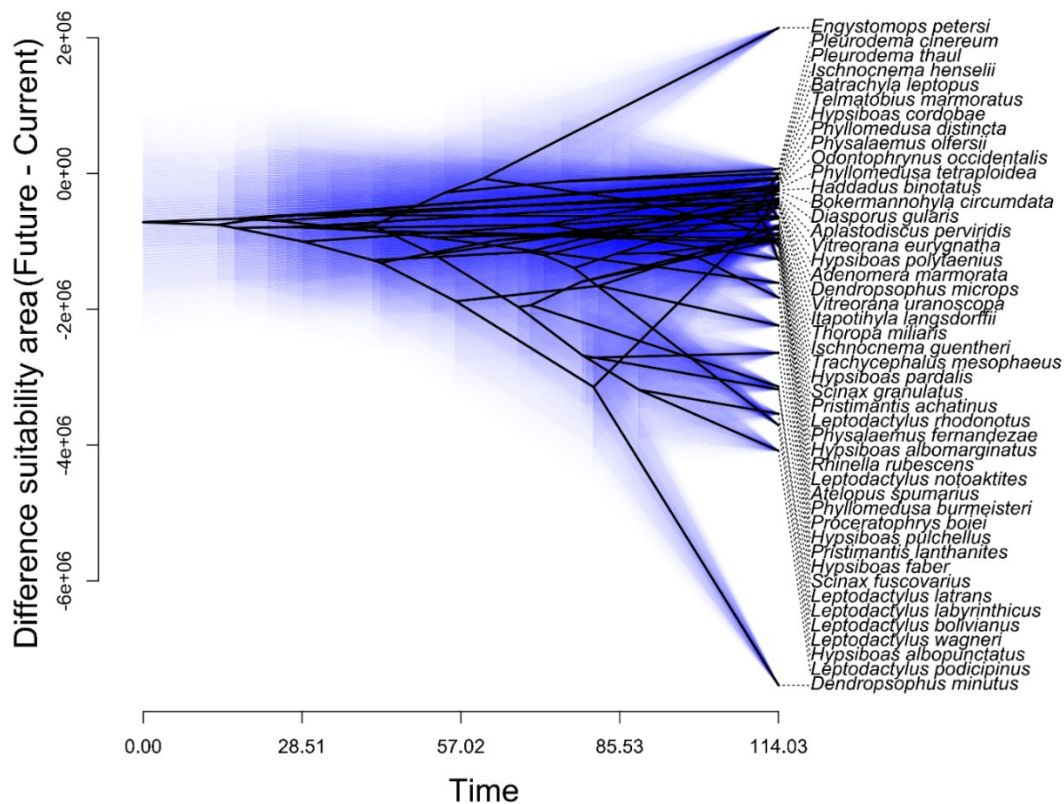


Figure 5 – Traitgram of suitability difference area (future-present) for native Neotropical species. Species with values above 0 will have an increase in their potential distribution, while species with values below 0 will have a decrease in their potential distribution when we compare the future and present scenarios.

Discussion

We found a large overlap in environmental suitability and niche between *Lc* and *Bd*, so *Lc* can host *Bd* without developing morbidity and mortality (Daszak et al. 2004b, Garner et al. 2006). Indeed, these frogs are resistant to infections with native strains of *Bd* (Urbina et al. 2018), suggesting a coexistence between these two species (Doddington et al. 2013). *Bd* has a global distribution (Olson et al. 2013, Van Rooij et al. 2015) and can benefit from climate change by encroaching on native species areas (Liu et al. 2013, Xie et al. 2016). Both *Bd* and *Lc* increased their areas in the future, even in a pessimistic scenario. Furthermore, there was an increase in the fitness-for-future overlap between these two species, reinforcing this host-pathogen relationship.

In contrast, although some native species show a high niche overlap with *Bd*, at

present (e.g. *Pristimantis achatinus*; $D = 0.64$), overall, there was a low environmental niche overlap between *Bd* and the native species, mainly for future scenarios. This may be due to chytridiomycosis, which can cause amphibian population declines (Voyles et al. 2009). In this case, *Lc* has been reported from more than 40 countries and is directly related to the decline of native species of several groups, including frogs (Kraus 2015, Pili et al. 2019). This can mature earlier in non-native environments and be reproductively active all year round (Leivas et al. 2012), what makes this species so successful are the pressures of individuals released into the environment (propagules) and tolerance to a wide range of climatic conditions (Rago et al. 2012).

In addition to emerging diseases, climate change plays a critical role as it is responsible for accelerating the loss of entire amphibian communities (Ron et al. 2003, Menéndez-Guerrero and Graham 2013). Therefore, it is vital to consider the synergistic effect of these threats to design conservation policies for neotropical amphibians. Thus, it is clear that the niche reduction for amphibians occurs due to multiple factors (e.g. environmental and species interaction) and, consequently, results in a reduction in species distribution (Soberón 2007, Holt 2009). It is known that species with reduced distributions are also sensitive to other types of threats and loss of genetic diversity and fitness (Holt 2009, Burke 2012, Martínez-Freiría et al. 2016). Even if it does not lead to mortality, the capacity of species to support *Bd* can vary in different environments (Zumbado-Ulate et al. 2019), with niche reduction in regions where the growth of the chytrid fungus is more favorable (Puschendorf et al. 2011).

We found moderate to large niche and suitability overlap between native and *Lc* species, with a decrease in the future. However, the area suitable in the future for *Lc* increased considerably, while that of native species reduced. Climate change can increase the dispersal of alien species (Bellard et al. 2013, Baquero et al. 2021), which can thrive

in environments outside their native ranges, increasing their competitive advantages (Pyšek et al. 2020). Here, future fitness for *Lc* increased, which is alarming for a highly adaptable species (Jancowski and Orchard 2013). This interaction between native species and *Lc* can result in several impacts, such as predation of native species (Wang et al. 2007), behavior modification resulting in loss of adaptability of native species (Heo et al. 2014), competition for resources (Kraus 2015), habitat displacement, changing the structure of native communities (Kenis et al. 2009) and decreasing the density and richness of native frogs (Li et al. 2011). For example, there are records of *Lc* predation on the species *Boana pulchella*, *Dendropsophus minutus*, *Leptodactylus latrans*, and *Scinax fuscovarius* (Boelter et al. 2012). These same species in our study obtained a high niche overlap with *Lc*. Thus, we can observe the direct impact of the bullfrog on Neotropical frog species, which may cause population declines, since it competes with other frogs for prey and microhabitat (Kats and Ferrer 2003), promotes acoustic competition (Medeiros et al. 2017), preys on other frog species (especially on metamorphic and young juvenile) (Kats and Ferrer 2003, Da Silva et al. 2011, Oda et al. 2019), in addition to also transport the chytrid fungus (Daszak et al., 2004).

In addition to the aforementioned observations, we observed a weak phylogenetic signal in the difference in suitable area for native species, indicating that closely related species tend to experience climate change in a similar way. Species can be affected in different ways by climate change, for example some species are expected to disperse to more suitable climatic areas. However, some species may benefit from climate change by expanding their suitable range area (Monzón et al. 2011), such as *Engystomops petersi* in our study. Ectotherms tend to be more affected by climate change and have less niche capabilities, obviously due to the lack of internal temperature control (Aragón et al. 2010). Therefore, large temperature variations can influence their survival (Bickford et al. 2010).

Thus, in the face of predicted climate changes, species may respond in different ways species (Kafash et al. 2018, Miller et al. 2018), that is, some will have a niche reduction, while others will maintain or even increase their amplitude (Urban 2015).

In our study we sought to understand how native species of neotropical frogs respond to climate change in terms of distribution and how this distribution relates to the presence of *Bd* and *Lc*. We noticed that by 2100 there is a tendency for these native species of frogs to lose a good portion of their distribution, as climate changes tend to increasingly reduce the areas suitable for these species, due to their physiological restrictions to the climate. However, this may not be the only impact suffered by Neotropical frog species. *Bd* is a species that can benefit from these climate changes, increasing its distribution and infecting frog species, causing chytridiomycosis. This was one of the findings in our work, which we predict an increase in the distribution for future scenarios of this species. Furthermore, it is expected that *Bd* is distributed exactly where most of the neotropical frog species are occurring. Furthermore, *Lc* exhibits similar behavior. Thus, we have a scenario where *Lc* can cause a great impact on natural populations of frogs, since it acts as a competitor, predator and vector of the chytrid fungus. Therefore, we have a synergistic effect of climate change, together with the intrinsic impacts of *Bd* and *Lc*, possibly promoting a great impact on the occurrence of several native species of frogs and even being able to extinguish many of them. Thus, we recommend interventions in conservation policies that consider the synergistic effect of climate change along with the occurrence of these species (*Bd* and *Lc*). In addition, modeling with these are welcome and recommended as they allow viewing future scenarios and the interaction with invasive species and emerging diseases, assisting in conservation strategies.

Declaration of Competing Interest

The authors declare they do not have any personal or financial conflict of interest that could influence the work reported in this article.

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Supplementary Information - Chapter 1

Influence of global climate change, invasive species and emerging diseases on native Neotropical frogs

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Supplementary Table S1. Climate variables in Bioclim dataset including codes, full names and units bio1~bio19 and elevation were the same as WorldClim dataset.

Code	Variables names	Unit
Bio1	Annual mean temperature	°C
Bio2	Mean diurnal range	°C
Bio3	Isothermality	%
Bio4	Temperature seasonality	°C
Bio5	Max temperature of warmest month	°C
Bio6	Min temperature of coldest month	°C
Bio7	Temperature annual range	°C
Bio8	Mean temperature of wettest quarter	°C
Bio9	Mean temperature of driest quarter	°C
Bio10	Mean temperature of warmest quarter	°C
Bio11	Mean temperature of coldest quarter	°C
Bio12	Annual precipitation	mm
Bio13	Precipitation of wettest month	mm
Bio14	Precipitation of driest month	mm
Bio15	Precipitation seasonality	%
Bio16	Precipitation of wettest quarter	mm
Bio17	Precipitation of driest quarter	mm
Bio18	Precipitation of warmest quarter	mm
Bio19	Precipitation of coldest quarter	mm
Alt	Mean elevation	meters

Supplementary Table S2. Accessible area based on morphoclimatic domains according to criteria of biogeographical regionalization of the Neotropical region selected according to the points of occurrence of Neotropical anuran species (Löwenberg-Neto 2014, Morrone 2014).

Species	Accessible area
<i>Adenomera marmorata</i>	Parana domain/Chacoan domain
<i>Aplastodiscus perviridis</i>	Parana domain/Chacoan domain
<i>Atelopus hoogmoedi</i>	Boreal Brazilian domain
<i>Batrachyla leptopus</i>	South American transition zone
<i>Boana albomarginata</i>	Parana domain/Chacoan domain
<i>Boana albopunctata</i>	All neotropic
<i>Boana cordobae</i>	Chacoan domain
<i>Boana faber</i>	Parana domain/Chacoan domain
<i>Boana pardalis</i>	Parana domain/Chacoan domain
<i>Boana polytaenia</i>	Parana domain/Chacoan domain
<i>Boana pulchella</i>	Parana domain/Chacoan domain/South brazilian domain/South American transition zone
<i>Bokermannohyla circumdata</i>	Parana domain/Chacoan domain
<i>Dendropsophus microps</i>	Parana domain/Chacoan domain
<i>Dendropsophus minutus</i>	All neotropic
<i>Diasporus gularis</i>	Pacific domain

<i>Engystomops petersi</i>	Boreal Brazilian domain/South American transition zone/Pacific domain/South brazilian domain/South-eastern Amazonian dominion
<i>Haddadus binotatus</i>	Parana domain/Chacoan domain/South brazilian domain
<i>Ischnocnema guentheri</i>	Parana domain/Chacoan domain
<i>Ischnocnema henselii</i>	Parana domain
<i>Itapotihyla langsdorffii</i>	Parana domain/Chacoan domain
<i>Leptodactylus bolivianus</i>	Boreal Brazilian domain Pacific domain South brazilian domain South eastern Amazonian dominion
<i>Leptodactylus labyrinthicus</i>	All neotropic
<i>Leptodactylus latrans</i>	All neotropic
<i>Leptodactylus notoaktites</i>	Parana domain/Chacoan domain
<i>Leptodactylus podicipinus</i>	Boreal Brazilian domain/Pacific domain/South brazilian domain/Parana domain/Chacoan dominion/South-eastern Amazonian dominion
<i>Leptodactylus rhodonotus</i>	South brazilian domain
<i>Leptodactylus wagneri</i>	Boreal Brazilian domain Pacific domain South brazilian domain South eastern Amazonian dominion - South America
<i>Odontophrynus occidentalis</i>	South American transition zone/Chacoan domain
<i>Phyllomedusa burmeisteri</i>	Parana domain/Chacoan domain
<i>Phyllomedusa distincta</i>	Parana domain
<i>Phyllomedusa tetraploidea</i>	Parana domain/Chacoan domain
<i>Physalaemus fernandezae</i>	Parana domain/Chacoan domain
<i>Physalaemus olfersii</i>	Parana domain
<i>Pleurodema cinereum</i>	South American transition zone/Chacoan domain/South brazilian domain
<i>Pleurodema thaul</i>	South American transition zone
<i>Pristimantis achatinus</i>	Boreal Brazilian domain/South American transition zone/Pacific domain
<i>Pristimantis lanthanites</i>	Boreal Brazilian domain/South American transition zone/Pacific domain/South brazilian domain
<i>Proceratophrys boiei</i>	Parana domain/Chacoan domain
<i>Rhinella rubescens</i>	Parana domain/Chacoan domain
<i>Scinax fuscovarius</i>	All neotropic
<i>Scinax granulatus</i>	Parana domain/Chacoan domain/South-eastern Amazonian dominion
<i>Telmatobius marmoratus</i>	South American transition zone/South brazilian domain
<i>Thoropa miliaris</i>	Parana domain/Chacoan domain
<i>Trachycephalus mesophaeus</i>	Parana domain/Chacoan domain
<i>Vitreorana eurygnatha</i>	Parana domain/Chacoan domain
<i>Vitreorana uranoscopa</i>	Parana domain/Chacoan domain

Supplementary Table S3. Values of the model performance metrics for each ensemble according to the modeled species (Bd, Lc and 46 neotropical frog species). BLOCK= Geographic partition structured as a checkerboard (a.k.a. block cross-validation). MAX TSS= Threshold at which the sum of the sensitivity and specificity is the highest. AUC= area under the ROC curve, TSS= true skill statistic.

Species	Partition	Threshold	AUC	TSS
<i>Adenomera marmorata</i>	BLOCK	MAX TSS	0.99	0.86
<i>Aplastodiscus perviridis</i>	BLOCK	MAX TSS	0.99	0.92
<i>Atelopus hoogmoedi</i>	BLOCK	MAX TSS	0.99	0.94
<i>Batrachochytrium dendrobatidis</i>	BLOCK	MAX TSS	1.00	0.96
<i>Batrachyla leptopus</i>	BLOCK	MAX TSS	0.99	0.95
<i>Boana albomarginata</i>	BLOCK	MAX TSS	0.99	0.93
<i>Boana albopunctata</i>	BLOCK	MAX TSS	0.98	0.92
<i>Boana cordobae</i>	BLOCK	MAX TSS	0.97	0.94
<i>Boana faber</i>	BLOCK	MAX TSS	0.99	0.96
<i>Boana pardalis</i>	BLOCK	MAX TSS	0.97	0.87
<i>Boana polytaenia</i>	BLOCK	MAX TSS	0.94	0.83
<i>Boana pulchella</i>	BLOCK	MAX TSS	1.00	0.96
<i>Bokermannohyla circumdata</i>	BLOCK	MAX TSS	0.98	0.93
<i>Dendropsophus microps</i>	BLOCK	MAX TSS	0.99	0.93
<i>Dendropsophus minutus</i>	BLOCK	MAX TSS	0.98	0.86
<i>Diasporus gularis</i>	BLOCK	MAX TSS	0.99	0.94
<i>Engystomops petersi</i>	BLOCK	MAX TSS	0.97	0.93
<i>Haddadus binotatus</i>	BLOCK	MAX TSS	0.98	0.89
<i>Ischnocnema guentheri</i>	BLOCK	MAX TSS	0.99	0.94
<i>Ischnocnema henselii</i>	BLOCK	MAX TSS	0.99	0.94
<i>Itapotihyla langsdorffii</i>	BLOCK	MAX TSS	0.92	0.79
<i>Leptodactylus bolivianus</i>	BLOCK	MAX TSS	0.99	0.94
<i>Leptodactylus labyrinthicus</i>	BLOCK	MAX TSS	0.99	0.94
<i>Leptodactylus latrans</i>	BLOCK	MAX TSS	0.99	0.92
<i>Leptodactylus notoaktites</i>	BLOCK	MAX TSS	1.00	1.00
<i>Leptodactylus podicipinus</i>	BLOCK	MAX TSS	0.99	0.92
<i>Leptodactylus rhodonotus</i>	BLOCK	MAX TSS	1.00	0.98
<i>Leptodactylus wagneri</i>	BLOCK	MAX TSS	0.98	0.91
<i>Lithobates catesbeianus</i>	BLOCK	MAX TSS	1.00	0.95
<i>Odontophrynus occidentalis</i>	BLOCK	MAX TSS	0.98	0.93
<i>Phyllomedusa burmeisteri</i>	BLOCK	MAX TSS	0.99	0.92
<i>Phyllomedusa distincta</i>	BLOCK	MAX TSS	0.99	0.91
<i>Phyllomedusa tetraploidea</i>	BLOCK	MAX TSS	0.99	0.94
<i>Physalaemus fernandezae</i>	BLOCK	MAX TSS	0.99	0.98
<i>Physalaemus olfersii</i>	BLOCK	MAX TSS	0.96	0.88
<i>Pleurodema cinereum</i>	BLOCK	MAX TSS	0.91	0.77
<i>Pleurodema thaul</i>	BLOCK	MAX TSS	0.99	0.98
<i>Pristimantis achatinus</i>	BLOCK	MAX TSS	1.00	0.94
<i>Pristimantis lanthanites</i>	BLOCK	MAX TSS	0.99	0.97
<i>Proceratophrys boiei</i>	BLOCK	MAX TSS	1.00	0.94
<i>Rhinella rubescens</i>	BLOCK	MAX TSS	0.96	0.86

<i>Scinax fuscovarius</i>	BLOCK	MAX TSS	1.00	0.98
<i>Scinax granulatus</i>	BLOCK	MAX TSS	0.99	0.94
<i>Telmatobius marmoratus</i>	BLOCK	MAX TSS	0.97	0.94
<i>Thoropa miliaris</i>	BLOCK	MAX TSS	1.00	0.98
<i>Trachycephalus mesophaeus</i>	BLOCK	MAX TSS	0.95	0.83
<i>Vitreorana eurygnatha</i>	BLOCK	MAX TSS	0.97	0.88
<i>Vitreorana uranoscopa</i>	BLOCK	MAX TSS	0.96	0.81

Supplementary Table S4. ODMAP (Overview, Data, Model, Assessment and Prediction) protocol

ODMAP element	Contents
OVERVIEW	
Autorship	<p>Authors: Philip Teles Soares¹, Daniel Paiva Silva, Diogo B. Provete Contact email: philip13ph@gmail.com Title: Influence of global climate change, invasive species and emerging diseases on native Neotropical frogs.</p>
Model objective	<p>Objective: Mapping/interpolation. Test the niche overlap and potential distribution of <i>B. dendrobatidis</i> and <i>L. catesbeianus</i> on neotropical frog species in the current and future climate change scenarios (2100)</p> <p>Target output: Maps of distribution presence for current and future scenarios.</p>
Taxon	<p>Invasive species: <i>Batrachochytrium dendrobatidis</i> (Fungi, Chytridiomycota, Rhizophydiales) and <i>Lithobates catesbeianus</i>.</p> <p>Neotropical native species: 46 frog species (Anura)</p>
Location	Global and Neotropical region.
Scale of analysis	<p>Spatial extent (Lon/lat): Global extent: -180, 180, -90, 83.645 (xmin, xmax, ymin, ymax); Neotropical extent: -118.405, -26.2422, -58.499, 32.717(xmin, xmax, ymin, ymax).</p> <p>Spatial resolution: 5 arc-minutes (~18.5 km at the equator) Temporal extent/time period: current: 1970 –2000, future: (CMIP6 – SSP8.5 for 2081–2100).</p>
Biodiversity data overview	<p>Observation type: GBIF database (http://www.gbif.org, accessed August 2020 – October 2021 – DOI: https://doi.org/10.15468/dl.a9nj77) and <i>B. dendrobatidis</i> occurrence data was provided by experts (courtesy of researchers Deanna H. Olson and Kathryn L. Ronnenberg, accessed July 2020).</p> <p>Response/Data type: Presence and background data.</p>
Type of predictors	19 climatic variables and elevation in WorldClim version 2.1 (https://www.worldclim.org/ ; accessed August 2020).
Conceptual model/hypotheses	Hypotheses about species-environment relationships:

	<p>- The Neotropics has high climatic suitability for invasive species while also harboring biodiversity hotspots (e.g., Cerrado, Atlantic Forest; Mittermeier et al., 2011), with a high richness of endangered species. This scenario suggests that amphibian diversity in the region can be highly impacted by climate change (Tylianakis et al. 2008, Gallardo et al. 2015), and infection by the chytrid fungus (Grant et al., 2016).</p>
Assumptions	<p>We assumed that:</p> <p>- i) the climatic niche of the invasive species and <i>Lithobates catesbeianus</i> (<i>Lc</i>) will overlap in the present and future with the fungus <i>Batrachochytrium dendrobatidis</i> (<i>Bd</i>) in the Neotropics; ii) The climatic niche of native species will overlap with that of <i>Bd</i> and <i>Lc</i>. We expect that regions with climate suitability for <i>Bd</i> and <i>Lc</i> will overlap with that for native species currently and in the future. This is due to the high dispersal and colonization abilities of <i>Lc</i> (Giovanelli et al. 2008, Nori et al. 2011). Finally, we expect that areas with climatic suitability for native species will be reduced.</p>
SDM algorithms	<p>Algorithms: general linear models (GLM; (Guisan et al. 2002), generalized additive model (GAM; (Guisan et al. 2002), boosted regression tree (BRT; Hijmans et al., 2017), maxent (MXS; (Phillips et al. 2006, Phillips 2017), Gaussian Process (GAU; (Weir and Pettitt 2000), random forest (RDF; (Cutler et al. 2007), maximum likelihood (MLK; (Royle et al. 2012) and support vector machine (SVM; Liu et al., 2010).</p> <p>Model complexity: Ensembles</p>
Model workflow	<ol style="list-style-type: none"> 1) Search and cleaning of occurrence data. 2) Download and format of climate data 3) Delimitation of study area (Neotropical region) 4) Training and calibration of models 5) Performance evaluation.
Software	<p>Software: Analyses were conducted in R version 4.0.2 (R Core Team 2021) with ENMTML package version 1.0.0 (de Andrade et al. 2020).</p> <p>Data availability: N/A</p>
DATA	
Biodiversity data	<p>Taxon names:</p> <p><u>Invasive species:</u> <i>Batrachochytrium dendrobatidis</i> and <i>Lithobates catesbeianus</i></p> <p><u>Neotropical native species (46 frog species):</u> <i>Adenomera marmorata</i>, <i>Aplastodiscus perviridis</i>, <i>Atelopus hoogmoedi</i>, <i>Batrachyla leptopus</i>, <i>Boana albomarginata</i>, <i>Boana albopunctata</i>, <i>Boana cordobae</i>, <i>Boana faber</i>, <i>Boana pardalis</i>, <i>Boana polytaenia</i>, <i>Boana pulchella</i>,</p>

	<p><i>Bokermannohyla circumdata, Dendropsophus microps, Dendropsophus minutus, Diasporus gularis, Engystomops petersi, Haddadus binotatus, Ischnocnema guentheri, Ischnocnema henselii, Itapotihyla langsdorffii, Leptodactylus bolivianus, Leptodactylus labyrinthicus, Leptodactylus latrans, Leptodactylus notoaktites, Leptodactylus podicipinus, Leptodactylus rhodonotus, Leptodactylus wagneri, Lithobates catesbeianus, Odontophrynus occidentalis, Phyllomedusa burmeisteri, Phyllomedusa distincta, Phyllomedusa tetraploidea, Physalaemus fernandezae, Physalaemus olfersii, Pleurodema cinereum, Pleurodema thaul, Pristimantis achatinus, Pristimantis lanthanites, Proceratophrys boiei, Rhinella rubescens, Scinax fuscovarius, Scinax granulatus, Telmatobius marmoratus, Thoropa miliaris, Trachycephalus mesophaeus, Vitreorana eurygnatha, Vitreorana uranoscopa.</i></p> <p>Ecological level: species</p> <p>Data source: GBIF database (http://www.gbif.org, accessed August 2020 – October 2021 – DOI: https://doi.org/10.15468/dl.a9nj77) and <i>B. dendrobatidis</i> occurrence data was provided by experts (courtesy of researchers Deanna H. Olson and Kathryn L. Ronnenberg, accessed July 2020).</p> <p>Sampling design: not applicable</p> <p>Sample size: The raw data contains a total of 5321 occurrences for the 46 Neotropical species, 1789 occurrences for <i>B. dendrobatidis</i> (worldwide) and 6059 occurrences for <i>L. catesbeianus</i> (worldwide). Altogether there are 13169 occurrences of species recorded by us.</p> <p>Regional mask: We clipped all data to the boundary of the study Neotropical region.</p> <p>Scaling: Occurrence were spatially thinned (within 10 kilometers) using spThin R package (Aiello-Lammens et al. 2015).</p> <p>Data cleaning/filtering: We cleaned data to avoid possible biases by removing i) duplicated records; ii) records with missing coordinates; iii) records falling on oceans using the package CoordinateCleaner ((Zizka et al. 2019). Additionally, we iv) filtered occurrence records from a minimum distance of 10 km to minimize sampling bias using the package spThin (Aiello-Lammens et al., 2015). Climate data</p>
Data partitioning	70% and 30% for calibration and evaluation.
Predictors variables	<p>Predictor variables: Climatic variables: Current and future scenario climatic variables (CMIP6 – SSP8.5 for 2081–2100) - Annual mean temperature, Mean diurnal range, Isothermality, Temperature seasonality, Max temperature of warmest month, Min temperature of coldest month, Temperature annual range, Mean temperature of wettest quarter, Mean temperature of driest quarter, Mean temperature of warmest quarter, Mean temperature</p>

	<p>of coldest quarter, Annual precipitation, Precipitation of wettest month, Precipitation of driest month, Precipitation seasonality, Precipitation of wettest quarter, Precipitation of driest quarter, Precipitation of warmest quarter, Precipitation of coldest quarter, Mean elevation.</p> <p>Data Sources: <i>WorldClim</i> version 2.1 https://www.worldclim.org/; accessed August 2020, (Fick and Hijmans 2017)</p> <p>Spatial resolution and extent of raw data: spatial resolution of 5 arc-minutes (~18.5 km at the equator).</p> <p>Geographic projection: proj= longlat, datum=WGS84</p> <p>Temporal resolution and extent of raw data: present (1970 –2000) and future scenario (2081–2100)</p> <p>Extent of raw data: Global extent: -180, 180, -90, 83.645 (xmin, xmax, ymin, ymax); Neotropical extent: -118.405, -26.2422, -58.499, 32.717(xmin, xmax, ymin, ymax).</p>
MODEL	
Variable pre-selection	
Multicollinearity	<p>We performed a principal component analysis (PCA) for the 19 bioclimatic and altitude variables. We used global (for <i>Lc</i> and <i>Bd</i>) and Neotropical extensions (native species of frogs) to develop models niche suitability.</p> <p>We retained the first six components (96% of variation) for the global models used in <i>Lc</i> and <i>Bd</i>. For the neotropical extension models for native species, we also retained the first six principal components (92% of variation).</p> <p>The 19 bioclimatic and altitude variables were first standardized with mean and variance equal to zero, and after that a PCA was generated, using the axes as new predictive variables in our global distribution (for <i>Lc</i> and <i>Bd</i>) and neotropical models (native species of frogs).</p>
Model estimates	Geographic partition structured as a checkerboard (a.k.a. block cross-validation).
Model averaging (Ensembles)	We use an ensemble (Araújo and New 2007) to calculate the average of the best models for each species by maximum True Skill Statistic – TSS.
Non Independence	Masking
ASSESSMENT	
Performance statistics	Performance statistics estimated on training data. Model performance was assessed based on the true skill statistic (TSS), area under a receiver operating characteristic (ROC) <i>curve</i> (AUC).
Plausibility checks	We checked model plausibility by assessing partial dependence plots.
PREDICTION	

Prediction output	Predictions of relative probability of presence expressed on a continuous and binary scale.
Uncertainty quantification	We accounted for algorithmic uncertainty by applying an ensemble approach averaging over four different SDM algorithms.

Chapter 2

Anthropogenic impacts and chytridiomycosis: synergistic effects of threats to neotropical frogs

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Abstract

Biodiversity loss is at the highest levels ever seen, with the rapid disappearance of species and ecosystem resources impacting human populations. One of the most threatened groups is amphibians. However, it is not known how frog diversity is affected by anthropic factors of land use and human population density, invasive species (such as *Lithobates catesbeianus* - *Lc*) and the chytrid fungus (*Batrachochytrium dendrobatidis* – *Bd*) on a neotropical scale. Thus, our work sought to answer the following questions: i) How are anthropogenic variables related to diversity patterns? ii) How does the distribution of *Lc* and *Bd* relate to anuran diversity patterns? iii) How do anthropogenic variables relate to the distribution patterns of *Lc* and *Bd*? We calculated taxonomic richness based on IUCN polygons and functional (FRic and FDiv) and phylogenetic (PD and MPD) richness and divergence indices. We used Geographically Weighted Regression to test the effect of land use and human population density variables on

Neotropical anuran diversity and map this relationship from the generated coefficients. Furthermore, we tested the occurrence of *Lc*, *Bd* and both species in relation to several facets of diversity using generalized least squares (GLS). Finally, we tested whether the anthropic variables addressed were related to the occurrence of *Bd* and *Lc*. We found that anthropic variables were negatively related to anuran diversity for almost the entire Neotropical region. Furthermore, we found that most of the diversity is located in regions where *Bd* is present. Thus, we expect that diversity will suffer both from the anthropization of its natural environments and from *Bd* infection. These threats must probably occur together, since the change in land use seems to favor the occurrence of both *Bd* and *Lc*, further increasing the impact on Neotropical frogs.

Keywords: Anura, different biodiversities, human population density, land use, threats to biodiversity, synergistic threats, chytrid fungus, dilution effect.

Introduction

Biodiversity loss is an urgent problem, influencing species distribution and abundance, loss of genetic diversity, and extinction (Pereira et al. 2012). The main drivers of biodiversity loss are habitat loss and fragmentation (Keil et al. 2015), overexploitation, the introduction of exotic species, climate change, and pollution (Young et al. 2016). A group particularly affected by habitat fragmentation (Becker et al. 2007) and changing land-use patterns (Nowakowski et al. 2018) is amphibians.

Amphibians are highly sensitive to environmental changes due to their behavior, physiology and life strategies, making them vulnerable to various threats such as habitat loss, climate change, invasive species and overexploitation of resources (Gaston 2005; Nowakowski et al. 2018; Semlitsch 2000). According to the IUCN Red List of Threatened Species (IUCN, 2020), amphibians are the most threatened vertebrates, and more than

30% of species are currently threatened with extinction. Due to the high diversity of Neotropical amphibians and growing threats to the survival of this group, it is crucial to take protective measures, especially in areas of high diversity and significant human density (Becker et al. 2010).

The increasing human impact on natural habitats has caused global changes in species distribution patterns (Venter et al. 2016a, 2016b). The human footprint index (HFI) compiles data on various types of human pressures between 1993–2009, such as 1) built environments, 2) human population density, 3) electrical infrastructure, 4) cropland, 5) pasture, 6) roads, 7) railways, and 8) navigable waterways (see Venter et al. 2016b). The Neotropics is one of the regions most affected by anthropic action, with increasing land-use change (Venter et al. 2016a) due to land conversion for agriculture and urbanization. On the other hand, the Neotropical region has hotspots for biodiversity conservation (e.g., Cerrado, Atlantic Forest; Mittermeier et al. 2011), with a high richness of endangered endemic species. Thus, human actions can impact amphibian diversity in the region together with climate change (Gallardo et al. 2015). However, little is known about how alternative facets of amphibian diversity are affected by land-use change.

Richness has been used as a synonym for biological diversity, being constantly used to delimit priority areas for species conservation (Jenkins et al. 2013). However, richness alone may not be enough to capture all the biodiversity and outline the best plans for the conservation of species, since it leaves aside the life history of species and their intrinsic characteristics (Brown et al. 2015, Brum et al. 2017). Functional diversity reflects the pool of ecological, morphological and physiological characteristics of species in a community (Petchey and Gaston 2002, 2006). In this case, we have for example the FRic metric, which is the amount of variability of the trait and also the FDiv, which are the degrees of divergence in the abundance distribution of the traits, in addition to other

functional metrics (Villéger et al. 2008). Phylogenetic diversity, in turn, or also evolutionary history, evokes how unique lineages are over deep evolutionary time (Faith 1992), and allows predicting how susceptible groups of species may be to extinction events (Purvis et al. 2000), being of great importance in the conservation of species (Winter et al. 2013). We have as metrics the phylogenetic richness (PD), which is a measure of the amount of evolutionary history in each community, and the mean paired distance (MPD), which measures the phylogenetic divergence and other metrics (Webb et al. 2002). Thus, it is interesting from the point of view of species conservation to consider these three dimensions of diversity, allowing greater predictive power of threats to biological diversity and ensuring better measures for conservation (Brum et al. 2017).

Recent studies showed that changes in land use decrease taxonomic and phylogenetic diversity (Nowakowski et al. 2018) and increase functional homogenization of communities (Nowakowski et al. 2017). However, the additive effect of the human footprint, invasive species, and emerging diseases on the distribution of multiple amphibian diversity patterns has not been tested before. Analyzing multiple dimensions of diversity can provide more robust predictive power for understanding how environmental changes affect biodiversity (Cianciaruso et al. 2009). Additionally, the use of multiple facets of diversity can be interesting to understand the geographic patterns of these facets and point out regions with high congruence for conservation (Brum et al. 2017). For example, in the Neotropical region, the Amazon and the Atlantic Forest have a high congruence of these three dimensions of diversity for mammals, however, there are still many areas that need not be under environmental protection and from which a great diversity resides (Brum et al. 2017). Overall, global threats to frogs have been acting together, causing multiple negative effects, such as habitat fragmentation, home range reduction and even extinction events (Hof et al. 2011). However, it is not clear how these

threats are geographically related to the multiple metrics of diversity of Neotropical amphibians, nor how these threats are related to each other, possibly having negative synergistic effects on the biological communities of frogs in the Neotropics. This work aims to answer the following questions: i) How are anthropic variables spatially related to diversity patterns? We expect that regions with the greatest changes in land use will be negatively associated with diversity, as they can result in changes in species' natural habitat, habitat fragmentation and even local extinctions (Hamer and Parris 2011, Hof et al. 2011). ii) How does the potential distribution of *Lc* and *Bd* relate to patterns of neotropical anuran diversity? We expect that both *Bd* and *Lc* have an overlapping distribution with the diversity of Neotropical frogs, since they are invasive and widely spread across the globe and have the potential to cause the homogenization of frog species (Scheele et al. 2019). And finally, iii) how are anthropic variables related to the neotropical distribution patterns of *Lc* and *Bd*? We expect that the same variables that negatively affect neotropical frogs will be positively associated with the distribution of *Bd* and *Lc*, since changes in the natural environment may favor host species and disease vectors (Guo et al. 2019), increased risk of chytridiomycosis in the neotropics.

Methods

Occurrence data of neotropical frog species

Species composition was obtained by superimposing extent-of-occurrence polygons of species (available at <http://www.iucnredlist.org>) in a $1^\circ \times 1^\circ$ cells grid (~110 km \times 110 km at the Equator) covering the entire Neotropical region. This analysis was performed in the *letsR* package (Vilela and Villalobos 2015).

*Collects occurrence data of *Bd* and *Lc**

We compiled *Lc* occurrence data from the Global Biodiversity Information

Facility - GBIF database (<http://www.gbif.org>, accessed August 2020 – October 2021 – DOI: <https://doi.org/10.15468/dl.a9nj77>). For *Bd* occurrence data, they were obtained by requesting experts in the distribution of this species (courtesy of researchers Deanna H. Olson and Kathryn L. Ronnenberg, accessed July 2020). These data were collected worldwide between 1835 and 2014. We cleaned data to avoid possible biases by removing i) duplicated records; ii) records with missing coordinates; iii) records falling on oceans using the package *CoordinateCleaner* (Zizka et al. 2019). Additionally, we iv) filtered occurrence records from a minimum distance of 10 km to minimize sampling bias using the package *spThin* (Aiello-Lammens et al., 2015).

Climate data for modelling Bd and Lc

For our climate predictor variables we downloaded data for 19 climate variables and elevation from WorldClim version 2.1 (<https://www.worldclim.org/>; accessed August 2020, (Fick and Hijmans 2017), with a spatial resolution of 5 arcminutes (~18.5 km at the equator) for the Neotropics to the present (1970 –2000), with global extent.

Obtaining land use and human density variables data

The HFI (Venter et al. 2016a) is a set of layers on human population density, land use, infrastructure (e.g., built-up areas, night lights, land use/cover), and human access (e.g., coastlines, roads, railways, navigable rivers). These data are available in high resolution, compiling data with high resolution of 1 Km² (Venter et al. 2016a). We collect specific variables according to our neotropical grid for land use change data, such as 1) built environments, 2) croplands, 3) pasture lands, and 4) human population density. For each variable we average within our 1st × 1st cells grid (~110 km × 110 km at the Equator).

Diversity Measures

The taxonomic diversity was calculated as the species richness in each cell. We

compiled 2,069 anuran species distributed in the neotropical region according to IUCN maps. We gathered the following functional trait data from the AmphiBIO database (Oliveira et al. 2017): (i) habitat use (e.g., fossorial, terrestrial, aquatic, arboreal); (ii) body size (adult snout-vent length in mm); and (iii) reproductive strategy (e.g., presenting larval stage, oviparous with direct development, and viviparous; Table 1). We calculated two measures of functional diversity: richness (FRic) and divergence (FDiv), using the R package FD (Laliberté and Legendre 2010). We pruned the species list from a fully-sampled phylogeny (Jetz & Pyron, 2018). We calculated (Tucker et al. 2017) phylogenetic richness (PD), which is a measure of the amount of evolutionary history in each community, and mean pairwise distance (MPD), which measures phylogenetic divergence (WEBB et al. 2002) in the picante package (Kembelet al.2010) in R, version 4.0.2 (R Core Team 2021). We found for this dataset 1,954 species with phylogeny and functional attribute data.

Table 1 - Functional response traits used to calculate richness (FRic) and divergence (FDiv) and their ecological interpretation.

Traits	Variable	Definition	Ecologic function	Source
Habitat	Categorical	Overall vertical foraging stratum (fossorial, terrestrial, aquatic, arboreal). Ignores details about seasonal or ontogenetic changes.	Characterization measure of preferential habitat use of amphibian species: terrestrial, aquatic, arboreal, and fossorial.	Lion et al., 2019; Oliveira & Scheffers, 2019
Body size	Continuous	Maximum adult body size (in mm). In frogs, the body size is reported as snout to vent length (SVL).	Related to the characteristics of life history.	Olalla-Tárraga & Rodríguez, 2007; Peters, 1983
Reproductive mode	Categorical	Whether the species reproduce via direct larval development or is viviparous.	Development strategies are linked to humidity levels.	da Silva et al., 2012; Gomez-Mestre et al., 2012

Ecological niche modeling for Bd and Lc

Firstly, we performed a principal component analysis (PCA) for the 19 bioclimatic and altitude variables. We used global (for *Lc* and *Bd*) to develop models niche suitability. We retained the first six components (96% of variation) for the global models used in *Lc* and *Bd*. The 19 bioclimatic and altitude variables were first standardized with mean and

variance equal to zero, and after that a PCA was generated, using the axes as new predictive variables in our global distribution for *Lc* and *Bd*. We generated the distribution models of the species using the following modeling methods: general linear models (GLM; (Guisan et al. 2002), generalized additive model (GAM; (Guisan et al. 2002), boosted regression tree (BRT; Hijmans et al., 2017), maxent (MXS; (Phillips et al. 2006, Phillips 2017), Gaussian Process (GAU; (Weir and Pettitt 2000), random forest (RDF; (Cutler et al. 2007), maximum likelihood (MLK; (Royle et al. 2012) and support vector machine (SVM; Liu et al., 2010).

We generated models for *Bd* and *Lc* for the whole world and then cropped them to the Neotropics to be able to relate to data on land use, human population density, and multiple diversities. All niche models were generated in the *ENMTML* package version 1.0.0 (de Andrade et al. 2020). We estimated the maximum True Skill Statistic (TSS - (Allouche et al. 2006), which ranges from -1 to 1, with models close to 1 considered excellent models, while negative models or close to zero are bad ones. Finally, we use an ensemble (Araújo and New 2007) to calculate the average of the best models for each species.

Data analysis

We tested whether the diversity (species richness, PD, MPD, FRic and FDiv) of neotropical frogs is influenced by anthropic variables (built environments, croplands, pasture lands and human population density) using geographically weighted regression (GWR) – (question 1). The GWR is a local spatial statistical approach, aiming to explore non-stationarity, built based on Generalized Linear Models, however incorporating local spatial relationships in the model. It is a locally weighted non-parametric analysis, in which the local regression parameters are estimated from subsets of data close to a model estimation point in the variable space (Wheeler and Páez 2009). Thus, the GWR allows

examining the relationships between a response variable and predictor variables and their variation in space, adjusting the regression coefficients for each spatial unit (Fotheringham et al. 2003). For this, it is necessary to create a local weighting matrix from the local observations (using our geographic coordinates), to estimate the local parameters. To create a local weighting matrix, we used the `gwr.sel` function from the `spgwr` package (Bivand et al. 2017), which allows the selection of the best spatial weighting matrix for the fit, minimizing the mean squared error of the models. From there, we generate our models using the `gwr` function from the `spgwr` package (Bivand et al. 2017). The results obtained in the GWR were exported and used to create maps with the spatial variation of the model coefficients. The maps were performed from the `tmap` package (Tennekes 2018).

We tested the differences of multiple diversities (response variable) in the patterns of occurrence of the invasive species addressed (factors: *Bd*, *Lc*, *Bd + Lc* and absence of species - AS) using generalized least squares (GLS) (Zuur et al. 2009) with restricted maximum likelihood estimation (REML) - (question 2). We chose correlation structures (exponential correlation – `corExp`; Gaussian correlation – `corGaus`; linear correlation – `corLin`; rational quadratic correlation – `corRatio`; spherical correlation – `corSpher`) using the Akaike Information Criteria (AIC) (Burnham and Anderson 1998). Analyses were performed using the “`nlme`” package (Pinheiro et al. 2017). For the pairwise comparisons we performed the *post hoc* test compatible with the GLS models from the `emmeans` package (Lenth et al. 2019).

Finally, we tested the occurrence of *Bd*, *Lc* and both species (*Bd + Lc*) in relation to the variables of land use and human population density from Generalized Linear Models (GLM; (McCullagh and Nelder 2019) - (question 3). For each model we use a distribution binomial with a logistic link function. All analyses, graphs and maps were

performed using the free software R version 4.0.2 (R Core Team 2021).

Results

Our results showed that the anthropic variables of land use and human density explained most of the richness of neotropical frogs (Quasi Global $R^2= 0.97$, $F= 1.834$, $df=2017_{(1448.1)}$, $P <0.0001$, table 2). Among the addressed variables, only built environments and human population density explained richness (Table 2). The maps generated from the GWR show negative coefficients for practically the entire Neotropical region (with the exception of a small region located in the Amazon region) of the relationship between frog richness and built environments (Figure 1A). However, the relationship between frog richness and human population density shows a different local pattern. The human population density presents negative local coefficients for several regions of the neotropical region. However, the region that today comprises the Atlantic Forest shows positive local coefficients between frog richness and human population density (Figure 1P).

The PD of neotropical frogs was also highly explained by land use and human density variables (Quasi Global $R^2= 0.98$, $F= 1.831$, $df=2017_{(1454.5)}$, $P <0.0001$, table 2). Very similar to the analyzed richness patterns, the significant variables in our models for PD were built environments and human population density (Table 2). In general, the local coefficients for the relationship between built environments and PD are negative, but in the Amazon region a small region with positive coefficients is visible (Figure 1B). For the relationship between PD of neotropical frogs and human population density, it is noted that in general there is a predominance of negative coefficients, however in the Atlantic Forest region and in a small region of the Amazon there are positive coefficients of this relationship (Figure 1Q).

The MPD of for neotropical frogs also had a high degree of explanation by our

analyzed anthropic variables (Quasi Global $R^2 = 0.88$, $F = 2.853$, $df = 2017_{(900)}$, $P < 0.0001$, table 2), however, in our global models now the variables croplands and human population density were significant. The generated maps of the relationship between cropland and MPD generally show negative local coefficients, but in a small region south of the Neotropical region it is possible to recognize positive coefficients (Figure 1H). For the relationship between MPD and human population density, it is possible to recognize mixed patterns, with several regions with negative and positive coefficients (although these are low values, see figure 1R).

Our models also found a large explanation of anthropic variables in relation to FRic (Quasi Global $R^2 = 0.93$, $F = 2.758$, $df = 2017_{(967.54)}$, $P < 0.0001$, table 2). However, only the human population density was significant in our models (Table 2). The GWR maps of this relationship showed that there are regions with positive coefficients, such as the Atlantic Forest, the Amazon and even regions such as the Cerrado. However, we have other regions with negative coefficients of this relationship (Figure 1S).

Similar to MPD, FDiv had a high degree of explanation by our anthropic variables (Quasi Global $R^2 = 0.88$, $F = 2.853$, $df = 2017_{(955.1)}$, $P < 0.0001$, table 2), with the variables croplands and human population density being significant. From the generated maps, we verified that most of the Neotropics show negative coefficients for the relationship between FDiv in relation to croplands (Figure 1I) and regions with positive and negative coefficients for human population density (Figure 1T).

We also created species distribution models for both *Bd* and *Lc* (Figure 2). The distribution models performed excellently for *Bd* (TSS = 0.96) and for *Lc* (TSS = 0.95, Figure 2). From these models, the presence and absence matrices of *Bd* and *Lc* could be constructed based on the Neotropical grid and correlated with the diversity facets and also with the anthropic variables. The results are below.

Table 2 - Global GWR between the different facets of diversity concerning land use and human density. * $P < 0.05$.

Variables	Quasi global R ²	F	df	P-value
Richness vs. land use and human density	0.97	1.834	2017 _(1448.1)	<0.0001*
(Intercept)		15.548		<0.0001*
Built environments		7.063		<0.0001*
Croplands		0.826		0.7649
Pasture lands		0.743		0.5974
Human population density		3.523		<0.0001*
PD vs. land use and human density	0.98	1.831	2017 _(1454.5)	<0.0001*
(Intercept)		0.842		0.5294
Built environments		4.926		<0.0001*
Croplands		0.670		0.9411
Pasture lands		0.743		0.5973
Human population density		3.442		<0.0001*
MPD vs. land use and human density	0.88	2.853	2017 ₍₉₀₀₎	<0.0001*
(Intercept)		0.877		0.6624
Built environments		0.839		0.7025
Croplands		3.370		<0.0001*
Pasture lands		0.109		1.0000
Human population density		1.778		<0.0001*
FRic vs. land use and human density	0.93	2.758	2017 _(967.54)	<0.0001*
(Intercept)		1.435		0.04751
Built environments		1.089		0.33905
Croplands		0.846		0.77918
Pasture lands		0.423		0.96989
Human population density		3.934		<0.0001*
FDiv vs. land use and human density	0.84	2.518	2017 _(955.1)	<0.0001*
(Intercept)		1.316		0.1051
Built environments		1.316		0.1243
Croplands		2.517		<0.0001*
Pasture lands		0.165		0.9998
Human population density		2.088		<0.0001*

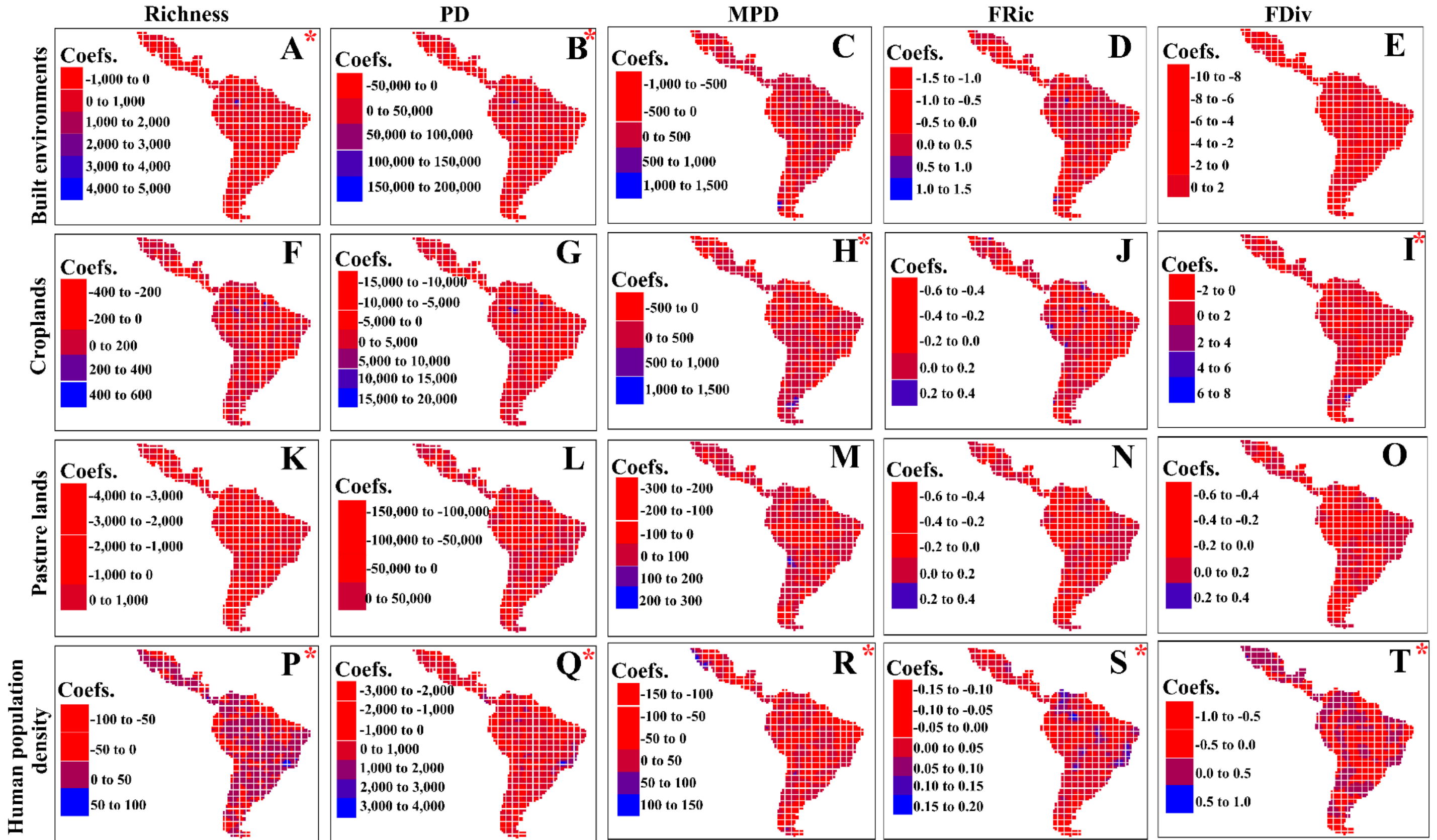


Figure 1 - Spatial distributions of the corresponding coefficients for the observed variables based on the GWR model for species richness, PD, MPD, FRic and FDiv of neotropical frogs in relationship: Built environments; Croplands; Pasture lands; and Human population density. * $P < 0.05$

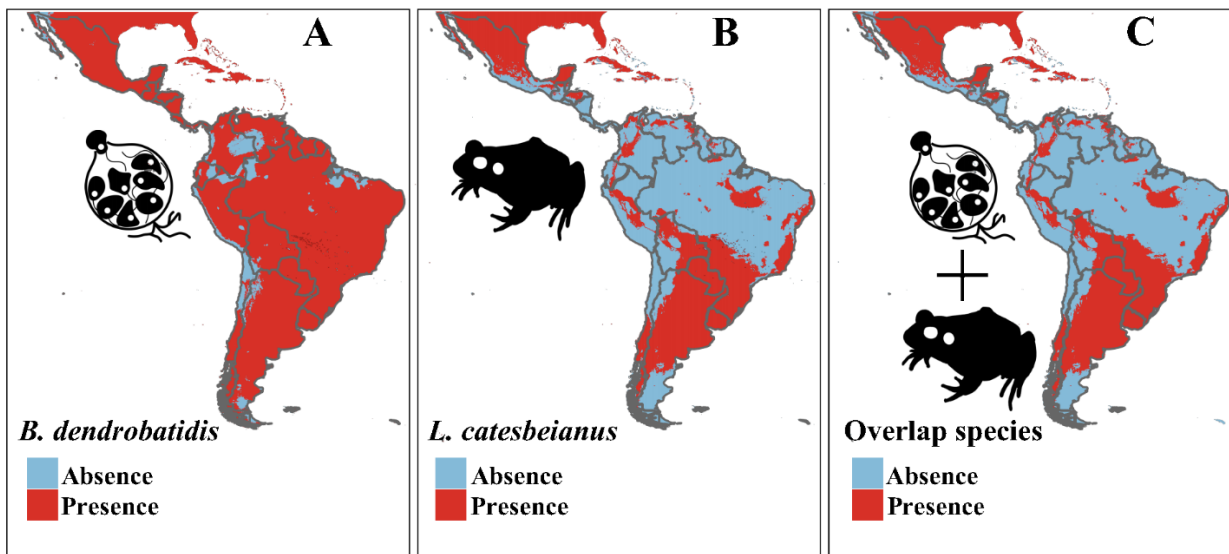


Figura 2 - Binary maps of species distribution models for: A) *Bd*, B) *Lc* and C) *Bd + Lc* overlay. All silhouettes were obtained from phylopic (<<http://phylopic.org/>>).

We found that the areas potentially only occupied by *Bd* showed higher values of Neotropical frog richness (mean= 61.2, sd= 33.7), followed by areas potentially occupied by both invasive species (*Bd + Lc*: mean= 42.1, sd=31.0; GLS: $F= 116.249$, $df=3$, $P<0.0001$; Figure 3A). The PD for Neotropical frogs follows a similar pattern of distribution. Areas potentially occupied only by *Bd* have higher PD values (mean= 3049, sd= 1513), followed by areas potentially occupied by both invasive species (*Bd + Lc*: mean= 2198, sd=1326; GLS: $F= 111.632$, $df=3$, $P<0.0001$; Figure 3B). The MPD was less in regions where *Lc*, *Bd* or both species would potentially not occur (absence invasive species: mean= 183, sd= 95; *Lc + Bd*: mean= 207, sd= 35.8, *Lc*: mean= 272, sd= 21.6, *Bd*: mean= 198, sd= 45.4; GLS: $F= 19.124$, $df=3$, $P<0.0001$; Figure 3C). Areas potentially occupied only by *Bd* showed the lowest values of FRic, however regions potentially occupied by *Bd* and *Bd + Lc* obtained higher values for Fric when compared to regions potentially not occupied by these species (absence invasive species: mean= 0.106, sd= 0.102; *Lc + Bd*: mean= 0.127, sd= 0.093, *Lc*: mean= 0.021, sd= 0.022, *Bd*: mean= 0.172, sd= 0.099; GLS: $F= 45.846$, $df=3$, $P<0.0001$; Figure 3D). Finally, FDiv was lower in regions without the presence of *Lc*, *Bd* or both (absence invasive species: mean= 0.6, sd= 0.337; *Lc + Bd*: mean= 0.785, sd= 0.139, *Lc*: mean= 0.825, sd= 0.022, *Bd*: mean= 0.732, sd= 0.204; GLS: $F= 75.641$, $df=3$, $P<0.0001$; Figure 3E). It is also interesting to note that all regions without the presence of invasive species had lower diversity values

(rich, PD, MPD, FRic and FDiv) than regions with the presence of only *Bd* or both species (*Bd+Lc*) (Figure 3).

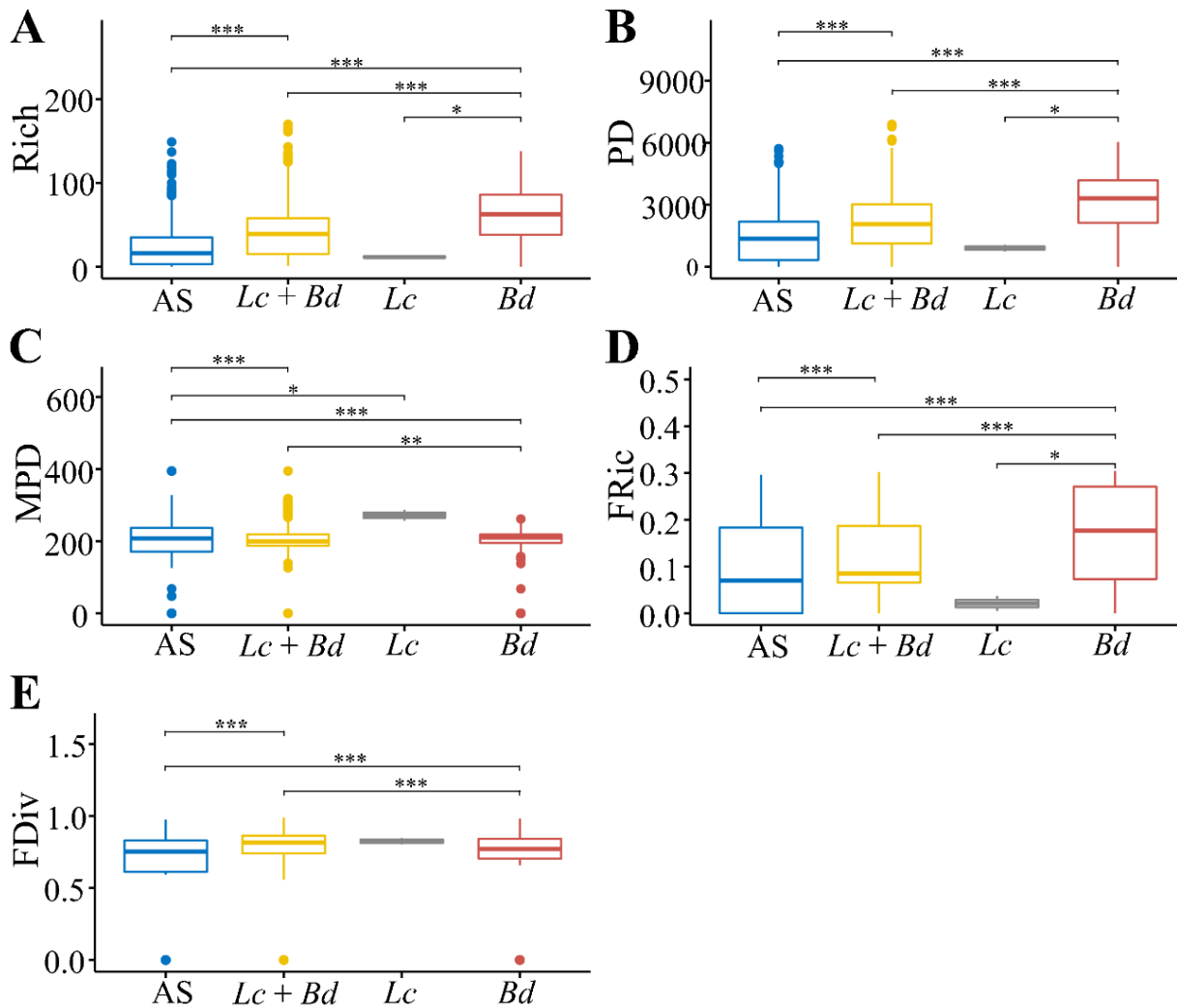


Figura 3- Box plot of the GLS models showing the occupation areas of invasive species: AS - absence invasive species; Lc + Bd - potential occurrence of *L. catesbeianus* and *B. dendrobatidis*; Lc - potential occurrence of *L. catesbeianus*; Bd - potential occurrence of *B. dendrobatidis*. A) Relationship between Rich x occupation areas of invasive species. B) Relationship between PD x areas of occupation of invasive species. C) Relationship between MPD x areas occupied by invasive species. D) Relationship between FRic x areas of occupation of invasive species. E) Relationship between FDiv x areas of occupation of invasive species. * $p < 0.05$. ** $p < 0.001$. *** $p < 0.0001$.

Our models show that regions with croplands ($Z = 9.659$, $P < 0.0001$; table 3; figure 4D) and pasture lands ($Z = 3.663$, $P = 0.0002$; table 3; figure 4G) can be positively related to the occurrence of *Bd*. On the other hand, population density is negatively associated with the distribution of *Bd* ($Z = -12.715$, $P < 0.0001$; table 3; figure 4J). The occurrence of *Lc* was also positively related to croplands

($Z= 8.330$, $P <0.0001$; table 3; figure 4E) and pasture lands ($Z= 9.995$; $P <0.0001$; table 3; figure 4H). Meanwhile, the occurrence of Lc is negatively related to built ($Z= -2.235$; $P =0.02$; table 3; figure 4B). Similarly, the combined occurrence of Lc and Bd is positively related to croplands ($Z= 8.343$, $P <0.0001$; table 3; figure 4F) and pasture lands ($Z= 10.023$, $P <0.0001$; table 3; figure 4I) and negatively related to built ($Z= -2.289$; $P <0.02$; table 3; figure 4C).

Table 3 - Binomial GLM relating the occurrence of Bd , Lc and $Bd + Lc$ in relation to the variables: Built environments; croplands; Pasture lands; and Human population density. * $P <0.05$.

Models	Estimate	Std. Error	Z	p-value
Binomial GLM Bd				
Intercept	1.491	0.066	22.582	<0.0001*
Built environments	-0.049	0.086	-0.566	0.5
Croplands	0.886	0.091	9.659	<0.0001*
Pasture lands	0.240	0.065	3.663	0.0002*
Human population density	-0.938	0.073	-12.715	<0.0001*
Binomial GLM Lc				
Intercept	-0.067	0.047	-1.441	0.1496
Built environments	-0.163	0.073	-2.235	0.02*
Croplands	0.441	0.052	8.330	<0.0001*
Pasture lands	0.489	0.048	9.995	<0.0001*
Human population density	0.074	0.059	1.247	0.2
Binomial GLM $Bd + Lc$				
Intercept	-0.072	0.047	-1.537	0.1243
Built environments	-0.169	0.074	-2.289	0.02*
Croplands	0.442	0.052	8.343	<0.0001*
Pasture lands	0.490	0.048	10.023	<0.0001*
Human population density	0.079	0.059	1.325	0.2

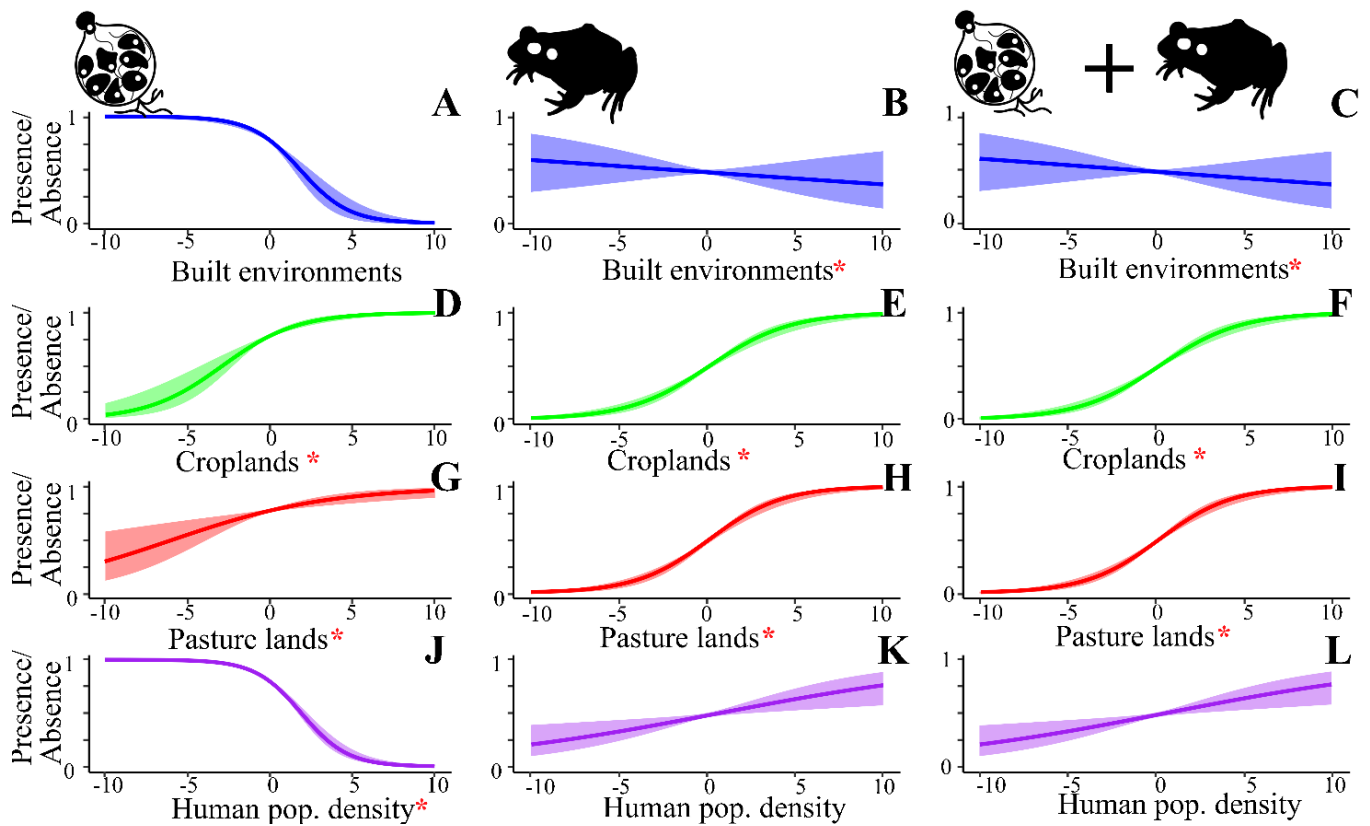


Figura 4 - Binomial GLM relating the occurrence of *B. dendrobatis*, *L. catesbeianus* and *Bd + Lc* in relation to the variables: Built environments; croplands; pasture lands; and Human population density. * p -value < 0.05. All silhouettes were obtained from phylopic (<<http://phylopic.org/>>).

Discussion

Our results showed interesting patterns (including spatial ones) of how different facets of diversity are affected and the risk that species diversity is under. We found in our study that there is a negative relationship between the species richness of neotropical frogs and built environments. In general, the conversion of natural environments to urban environments can trigger habitat loss and fragmentation of environments (Hamer and McDonnell 2008, Semlitsch and Skelly 2008), negatively affecting amphibian populations at local and broader scales (Hamer and Parris 2011, Yang et al. 2022). Urbanization is an important anthropic factor, as conversion to urban environments can lead to the direct loss of several species, mainly because few species can adapt to these modifications and survive (McDonnell and Hahs 2015). This is due to their complex life history and their physiological tolerances, which may make them susceptible to drastic changes in their habitats (Cushman 2006, Barrett and Guyer 2008). Amphibians are more sensitive to urban environments than other taxa (Hamer and McDonnell

2008b) due to their dependence on freshwater for development and transition to terrestrial life and their low dispersal abilities (Semlitsch 2000). Modification in urban areas can reduce available breeding sites (Westgate et al. 2015) and create unsuitable environments for amphibians, thus reducing the survival of juveniles and adults (Hamer and McDonnell 2008b, Sievers et al. 2018). Additionally, land-use changes can reduce frog populations, limiting suitable areas for persistence, reducing connectivity between habitats, negatively influencing dispersal and foraging, and promoting extinctions of local and regional populations (Mac Nally et al. 2009).

Our results also point to a negative relationship between PD and built environments in practically the entire neotropical region. Urbanization affects not only species richness (Concepción et al. 2016), but causes loss of functional (Nock et al. 2013) and phylogenetic diversity (Knapp et al. 2017, Callaghan et al. 2021). The changes caused by urbanization can reduce the population of frog species and the connectivity between their populations, in addition to low dispersion and narrow environmental tolerances, they can reduce the genetic diversity of these species (Cushman 2006). Thus, amphibian genetic diversity tends to decrease in urbanized regions (Homola et al. 2019, Wilk et al. 2020), however, there are cases in which genetic diversity can be maintained or even increased (Nowakowski et al. 2018, Wilk et al. 2020), evidencing the behavior of some species against the urbanization of natural environments. This may be related to the intrinsic characteristics of the species, as generalist species, which tend to be more tolerant of altered regions and low emission demand, may be more successful in urbanized regions. (Hamer and McDonnell 2008). Thus, urbanization may affect species less adapted to anthropic changes, which may affect particular lineages, reducing phylogenetic diversity in places with a high degree of urbanization (Callaghan et al. 2021).

Our results also showed that MPD in general has a negative relationship with cropland. In fact the conversion of natural areas into cropland and pasture may decrease not only species but also the phylogenetic diversity of species (Bonetti and Wiens 2014, Nowakowski et al. 2017, 2018). Clades that are more sensitive to environmental variation and/or strongly dependent on their habitats, especially

those with conserved traits, may have a reduction in their distribution due to changes in their sheltering, foraging and/or reproduction sites (Nowakowski et al. 2018). However, amphibians that breed in still water may be tolerant of habitat conversion. This is because these frogs can benefit from the creation of new water bodies created artificially by man (such as irrigation ponds, or rice farming), creating perfect habitats for reproduction and oviposition. (Gomez-Mestre et al. 2012). Thus, it is possible that there are regions with higher phylogenetic diversity values in regions with cropland and pasture land (Bonetti and Wiens 2014, Nowakowski et al. 2017, 2018).

Similar to MPD, FDiv was also negatively related to croplands over most of the Neotropical range. There is evidence that the same altered regions, such as crops or pastures, can maintain taxonomic diversity, depending on the quality of the environment and resource availability (Ndriantsoa et al. 2017, Nopper et al. 2017). However, it is expected that with changes in habitat and intensification of land use there will be a functional loss for several taxa, include frogs (Trimble and van Aarde 2014, Mumme et al. 2015, Almeida et al. 2016, Riemann et al. 2017, Etard et al. 2022). In this way, land use conversion not only tends to decrease frog populations, but may also decrease genetic diversity (Bonetti and Wiens 2014, Nowakowski et al. 2017, 2018) and functional diversity of these organisms. In addition, the conversion of land use to croplands can be accompanied by the intense use of fertilizers and pesticides (Hunke et al. 2015), which can promote DNA changes and the development of abnormalities in tadpoles, for example (Borges et al. 2019). Thus, we have a worrying scenario, since the loss of biodiversity will be greater in the Neotropics, due to the combined impacts of changes in land use and global climate change (Colwell et al. 2008, Gonçalves et al. 2021), which will reduce the availability of natural habitat such as one of the consequences is biodiversity (Staude et al. 2020). As a consequence of this, species with less capacity to adapt to these new environments and/or with capabilities to track more suitable climates will result in population declines and extinctions (Zamora-Gutierrez et al. 2018).

As a result, we found that all facets of diversity (Rich, PD, MPD, FRic and FDiv) were determined by human population density. We verified that several regions of the Neotropics presented

negative coefficients, which was a result we had already expected. However, regions of the Atlantic Forest, the Amazon and even parts of the Cerrado showed high positive coefficients for the relationship between diversity and human population density. This was an unexpected result of our predictions. Researchers argue that grain size can positively affect the relationship between diversity and human population density, especially when these grains are larger than 2,500 km² (Luck 2007). The congruence between biodiversity and human population density can also be explained by the energy availability, which benefits both (Evans and Gaston 2005, Gaston 2005). Also, the distribution of human population density may reflect geological and environmental factors, especially those linked to agricultural production (Kirch et al. 2004, Vitousek et al. 2004).

In our study, we found a wide potential distribution area for *Bd* and *Lc*, overlapping with several areas with great diversity of neotropical frog species. Amphibian diversity has suffered declines over the last few years (Pimm et al. 2014, Ceballos et al. 2020), due to several factors, such as global climate change (Daufresne et al. 2009, Li et al. 2013), changes in land use (including anthropogenic pressures such as those discussed above) (Hof et al. 2011), chytridiomycosis (Bellard et al. 2016, Doherty et al. 2016) and interaction with invasive species, especially the interactions with *Lc* (Kraus 2008). Thus, for neotropical species of frogs, according to our findings, a synergistic effect between the impacts of land use change, human population density, chytridiomycosis and invasive species (as is the case of *Lc*) on diversity is expected (Hof et al. 2011). Chytridiomycosis, for example, is responsible for several outbreaks of infection, causing global population declines of at least 501 species and even extinguishing around 90 amphibian species in the 21st century (Scheele et al. 2019). Among these declines, about 150 species in South America have suffered such declines, with about 50 species in Brazil alone (which comprises much of the Neotropical region), mainly affecting species with a smaller range (Scheele et al. 2019). These impacts are of interest for conservation, as the effects of decline caused by *Bd* can affect not only amphibians, but also other taxa, and may result in a decrease in biodiversity via a trophic cascade (Zipkin and DiRenzo 2022).

We verified that most of the richness of Neotropical frogs are distributed in places with the potential presence of *Bd* and both species (*Bd* + *Lc*). In general, chytridiomycosis has been associated with worldwide declines in frogs (Bellard et al. 2016, Doherty et al. 2016). Several population declines in the Neotropics have been reported due to *Bd* infection (Lips et al. 2006, 2008, Lips 2016). For example, in the region comprising the Andes and Central America, frogs of the genus *Atelopus* have disappeared due to outbreaks of chytridiomycosis (Lips et al. 2006). In Brazil, for example, there are historical findings of chytridiomycosis and the relationship with amphibian populations, especially in the region comprising the Atlantic Forest, showing population declines and even the local extinction of some of these infected species (Carvalho et al. 2017). Thus, areas with high frogs richness rates are expected to be affected according to the potential distribution of *Bd* found in our findings, causing the local extinction of several species over time with exposure to this pathogen. Added to this, we can have a scenario where, in addition to the *Bd* fungus, we have an association with *Lc* in these places, which can contribute to a decrease in the species richness of frogs. We can expect this impact on richness because *Lc* is an invasive species, which is considered a voracious competitor (Leivas et al. 2012), in addition to being a generalist predator (it can even consume other frogs) (Toledo et al. 2007), and works as a vector for *Bd* (Schloegel et al. 2010), directly impacting the survival and reproduction of frogs natives.

We also found that, like richness, PD was higher in regions potentially occupied by *Bd* and both species (*Bd* + *Lc*), than in regions with absence of these species. Furthermore, we evidenced that the MPD of Neotropical frogs was lower in regions with absence of either *Bd*, *Lc* or both species. We highlight, as well as (Nowakowski et al. 2018), that the conversion of natural habitats into cropland sites, for example, can be important in the local extinction of specific clades, promoting as a consequence the phylogenetic homogenization of frogs. Here we emphasize that in addition to the impact of the conversion of these natural areas, we can have a synergistic effect of the action of *Bd* and *Lc* for the homogenization of phylogenetic diversity. In the region, for example, comprising Lower Central

America, extinctions of several species were found in a non-random way due to *Bd* infection, affecting species with little occupation and also endemic species (Smith et al. 2009). In addition, the complete loss of two families considered rare (Aromobatidae and Hemiphractidae) was diagnosed, suggesting that these losses are not random, causing the loss of the evolutionary history of frogs for this region and consequently the phylogenetic homogenization (Smith et al. 2009). In the Atlantic Forest region, for example, it has a high species richness and we also found the various effects for phylogenetic diversity, it has an occupation by *Bd* in our predictions. In this region reside more than 400 endemic species (Haddad et al. 2013), which may be affected by the synergistic effect of conversion of natural areas and *Bd* infection. There is a complex relationship between *Bd* infection and amphibians, from which there are variable population declines, where susceptibility to infection has a phylogenetic pattern of infection, ie, a phylogenetic signal (not tested in our studies) (Bielby et al. 2008, Baláz et al. 2014, Azat et al. 2022). In the South American region, the frog families most affected by *Bd* infection were mainly Ranidae, Odontophrynidae, Hylidae, Phyllomedusidae, Telmatobiidae, Hylodidae, Brachycephalidae, Hemiphractidae, Calyptocephalellidae and Pipidae (Azat et al. 2022).

Regions with the potential presence of *Bd* also showed higher values of FRic and FDiv than regions with the absence of invasive species in our findings. It is interesting that factors such as life history and behavior of amphibians can be determinant for survival against *Bd* infection (Berger et al. 2016). There appears to be greater susceptibility and population impacts in species with greater association with aquatic environments than drier and warmer environments (Bielby et al. 2008, Rowley and Alford 2013). In South America, there are indications that factors such as ecoregion, host characteristics (such as risk of extinction) and preferred habitat determine patterns of *Bd* infection. Regarding the preferred habitat type, there is a phylogenetic pattern associated with the species that are infected (Ranidae, Telmatobiidae, Hylodidae, Calyptocephalellidae and Pipidae), which have preferences for aquatic habitats (Azat et al. 2022). Other studies analyzing *Bd*-infected species around the world have shown that the severity of frog decline is more associated with species with larger body

sizes and which occur in wet regions with permanent aquatic habitats (Scheele et al. 2019). The association with the more prevalent *Bd* infection in species with preferentially aquatic life habits is already expected, since humid conditions are more favorable for the development and propagation of the fungus and in drier conditions there may be desiccation and lead to mortality of the fungus pathogen (James et al. 2015). Adults and tadpoles are susceptible to *Bd* infection, but for most species tadpoles do not show symptoms, but during the metamorphosis period there may be mortality. On the other hand, for other species, there may be symptoms of *Bd* infection by tadpoles, such as abnormality in the oral disc and depigmentation, which can lead to mortality (Berger et al. 2016). The *Bd* infection also has differential susceptibility according to ontogeny (Van Rooij et al. 2015). In this sense, infection in post-metamorphic frogs can induce morbidity and/or mortality conditions (Rachowicz and Vredenburg 2004). Other tadpoles (such as *Amerana muscosa*) can be infected with *Bd* and not develop symptoms (Rachowicz and Vredenburg 2004), while other species can be harmed by infection during the larval stage (Blaustein et al. 2005).

Our findings point to a greater diversity (richness, PD, MPD, FRic and FDiv) of Neotropical frogs in regions occupied by *Bd*. Although we expect scenarios where there will be a loss of diversity, we can also address other effects of this interaction. One of these scenarios is based on the phenomenon that increasing biodiversity can result in reduced risk of infectious diseases, called the “dilution effect” (Keesing et al. 2010, Halliday and Rohr 2019). Thus, the dilution effect proposes that communities with greater diversity have the capacity to inhibit the abundance of parasites through different mechanisms, such as interference in the parasite transmission process or even in the regulation of host populations susceptible to infection (Keesing et al. 2010, Rohr et al. 2020). Therefore, the more diverse the community, the smaller the proliferation of parasites tends to be, thus ensuring the stability of ecological communities and ecosystem services (Boyd et al. 2013). On the other hand, we can also expect that the loss of biodiversity can favor the proliferation of pathogens and the incidence of infectious diseases (Keesing et al. 2010, Rohr et al. 2020). Experimental evidence already suggests that

there is a dilution effect on the relationship between amphibians and *Bd* (Searle et al. 2011, Venesky et al. 2014a). Thus, if this diversity of amphibians really contributes to reducing the risk of *Bd* infection, it is important to establish research to identify habitats and communities that have a higher risk of chytridiomycosis outbreaks (Venesky et al. 2014b).

Our study also contributes with this information about the effect of dilution. We point out that there is a positive relationship of the potential distribution of *Bd* and *Lc* with the land use variables croplands and pasture lands. In this sense, we expect that these variables may favor the permanence of *Bd* and *Lc* and negatively impact the diversity of Neotropical frogs. Thus, we can have the negative synergistic effect of *Bd* infection, interaction of native species with *Lc* and changes in land use, which may affect the diversity of Neotropical frogs. In general, agriculture and habitat fragmentation tend to benefit host and vector species, which may be responsible for increasing disease risk (Guo et al. 2019). In addition, dense host populations resulting from increased urbanization and agriculture can promote the evolution of more virulent and resistant parasites (Rogalski et al. 2017). However, for the Atlantic Forest region, although there was a decrease in diversity in altered areas (in this case for microorganisms on the skin of frogs), there was a higher prevalence for *Bd* in natural areas (Becker et al. 2017). In view of this, we hope that this study can provide information to face the threats to the biodiversity of neotropical frogs, since we point out how changes in land use can affect the different facets of diversity and how the potential distribution of *Bd* and *Lc* can relate to this data. In addition, we hope that this information brought by this work can be relevant in the internal policies of countries like Brazil, which in recent years have left something to be desired in actions against deforestation, going against the grain of species conservation, creating an alarming scenario that deserves attention from researchers and policy makers for the preservation of biodiversity in the neotropical region.

Finally, our work shows that there are different threats affecting multiple dimensions of neotropical diversity (taxonomic, functional and phylogenetic) of frogs and that these threats are differentially related in space. These threats are characterized by the fragmentation and alteration of

natural environments, which can result in the loss not only of species, but of functional attributes and entire groups of species. Added to this, we have the impacts of the possible occupation of chytridiomycosis together with *Lc*, which may occupy precisely regions with great diversity of Neotropical frogs, promoting the homogenization of the diversity of neotropical frogs via skin diseases (affecting from tadpoles to adults) and causing a possible decline in this region. Furthermore, changes in the environment can even favor both invasive species, such as *Lc*, and create favorable environments for the propagation of *Bd*, resulting in a negative synergistic effect for the diversity of neotropical frogs.

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Conclusão geral

Multiplas ameaças são conhecidas que causam o declínio de espécies de anfíbios. Isso já se sabe. No entanto, o nosso trabalho avaliou de que forma essas múltiplas ameaças podem impactar sinergicamente a distribuição e a diversidade de sapos neotropicais. As mudanças climáticas são consideradas com um forte preditor para o declínio de sapos, principalmente porque esses animais possuem restrições ótimas estreitas e podem não se adaptar a mudanças no clima. Porém, além do impacto da diminuição da distribuição, os sapos neotropicais podem enfrentar a interação negativa com a rã-touro, que é uma espécie competidora melhor, um predador pra muitas espécies de sapos e também um vetor do fungo quitrídio. O fungo quitrídio por sua vez age causando declínios populacionais globais a algum tempo. Tanto o *Bd*, quanto o *Lc* possuem aumento de áreas adequadas em nossas previsões de acordo com as mudanças climáticas. No entanto, esse cenário não é o mesmo para grande parte dos anuros amostrados em nossas análises. Esse cenário é ainda mais preocupante, pois existe uma sobreposição de nicho e de áreas adequadas quando comparamos o *Bd* e a *Lc* com as espécies nativas de sapos neotropicais. Assim, podemos ter o efeito sinérgico das mudanças climáticas e do fungo quitrídio e da rã-touro, impactando negativamente as espécies de sapos. Avaliamos também como as diferentes dimensões da diversidade (taxonômica, funcional e filogenética) se relacionam espacialmente com variáveis antrópicas como mudanças no uso do solo e densidade populacional humana. A diversidade em geral responde negativamente as variáveis antrópicas em diversas regiões da região neotropical. Assim, essas variáveis antrópicas podem resultar na fragmentação e diminuição do hábitat natural dos anuros neotropicais, podendo resultar não somente na perda de espécies, mas de atributos funcionais e até mesmo da história de vida desse grupo, uma vez que grupos inteiros podem ser extintos. Além disso, encontramos em nossos resultados que a maior parte da diversidade (taxonômica, funcional e filogenética) está distribuída justamente em regiões onde o fungo quitrídio pode potencialmente ocorrer. Logo, esperamos que haja dois efeitos sinérgicos negativos para a diversidade de anuros neotropicais, pois o *Bd* pode impactar negativamente, por meio das extinções locais que provoca. Assim, podemos ter

sérios riscos a diversidade com todas essas ameaças agindo juntamente e promovendo a homogeneização da diversidade biológica. Diante disso, é necessário criar planos de conservação que contemplem o efeitos sinérgico dessas ameaças para garantir um maior sucesso na conservação desse grupo de espécies e impedir próximos declínios no futuro.

Referências

- Aiello-Lammens, M.E.; Boria, R.A.; Radosavljevic, A.; Vilela, B.; Anderson, R.P. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545.
- Allouche, O.; Tsoar, A.; Kadmon, R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology* 43: 1223–1232.
- Almeida, S.M.; Silva, L.C.; Cardoso, M.R.; Cerqueira, P.V.; Juen, L.; Santos, M.P. 2016. The effects of oil palm plantations on the functional diversity of Amazonian birds. *Journal of Tropical Ecology* 32: 510–525.
- de Andrade, A.F.A.; Velazco, S.J.E.; Júnior, P.D.M. 2020. ENMTML: An R package for a straightforward construction of complex ecological niche models. *Environmental Modelling & Software* 125: 104615.
- Aragón, P.; Rodríguez, M.A.; Olalla-Tárraga, M.A.; Lobo, J.M. 2010. Predicted impact of climate change on threatened terrestrial vertebrates in central Spain highlights differences between endotherms and ectotherms. *Animal Conservation* 13: 363–373.
- Araújo, M.B.; New, M. 2007. Ensemble forecasting of species distributions. *Trends in ecology & evolution* 22: 42–47.
- Araújo, M.B.; Thuiller, W.; Pearson, R.G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of biogeography* 33: 1712–1728.
- Azat, C.; Alvarado-Rybak, M.; Solano-Iguaran, J.J.; Velasco, A.; Valenzuela-Sánchez, A.; Flechas, S.V.; et al. 2022. Synthesis of Batrachochytrium dendrobatidis infection in South America: amphibian species under risk and areas to focus research and disease mitigation. *Ecography* 2022: e05977.
- Baláz, V.; Voeroes, J.; Civiš, P.; Vojar, J.; Hettyey, A.; Sos, E.; et al. 2014. Assessing risk and guidance on monitoring of Batrachochytrium dendrobatidis in Europe through identification of taxonomic selectivity of infection. *Conservation Biology* 28: 213–223.
- Baquero, R.A.; Barbosa, A.M.; Ayllón, D.; Guerra, C.; Sánchez, E.; Araújo, M.B.; et al. 2021. Potential distributions of invasive vertebrates in the Iberian Peninsula under projected changes in climate extreme events. *Diversity and Distributions* 27: 2262–2276.
- Barnosky, A.D.; Matzke, N.; Tomiya, S.; Wogan, G.O.; Swartz, B.; Quental, T.B.; et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.
- Barrett, K.; Guyer, C. 2008. Differential responses of amphibians and reptiles in riparian and stream habitats to land use disturbances in western Georgia, USA. *Biological conservation* 141: 2290–2300.
- Becker, C.G.; Longo, A.V.; Haddad, C.F.B.; Zamudio, K.R. 2017. Land cover and forest connectivity alter the interactions among host, pathogen and skin microbiome. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170582.
- Becker, C.G.; Fonseca, C.R.; Haddad, C.F.B.; Batista, R.F.; Prado, P.I. 2007. Habitat split and the global decline of amphibians. *Science* 318: 1775–1777.
- Bellard, C.; Genovesi, P.; Jeschke, J.M. 2016. Global patterns in threats to vertebrates by biological invasions. *Proceedings of the Royal Society B: Biological Sciences* 283: 20152454.
- Bellard, C.; Thuiller, W.; Leroy, B.; Genovesi, P.; Bakkenes, M.; Courchamp, F. 2013. Will climate change promote future invasions? *Global change biology* 19: 3740–3748.
- Berger, L.; Roberts, A.A.; Voyles, J.; Longcore, J.E.; Murray, K.A.; Skerratt, L.F. 2016. History and recent progress on chytridiomycosis in amphibians. *Fungal Ecology* 19: 89–99.
- Betts, M.G.; Wolf, C.; Ripple, W.J.; Phalan, B.; Millers, K.A.; Duarte, A.; et al. 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* 547: 441–444.
- Bickford, D.; Howard, S.D.; Ng, D.J.J.; Sheridan, J.A. 2010. Impacts of climate change on the amphibians and reptiles of Southeast Asia. *Biodiversity and Conservation* 19: 1043–1062.

- Bielby, J.; Cooper, N.; Cunningham, A.; Garner, T.W.J.; Purvis, A. 2008. Predicting susceptibility to future declines in the world's frogs. *Conservation Letters* 1: 82–90.
- Bivand, R.; Yu, D.; Nakaya, T.; Garcia-Lopez, M.-A.; Bivand, M.R. 2017. Package 'spgwr.' *R software package*.
- Blaustein, A.R.; Romansic, J.M.; Scheessele, E.A.; Han, B.A.; Pessier, A.P.; Longcore, J.E. 2005. Interspecific variation in susceptibility of frog tadpoles to the pathogenic fungus *Batrachochytrium dendrobatidis*. *Conservation Biology* 19: 1460–1468.
- Blomberg, S.P.; Garland Jr, T.; Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717–745.
- Boelter, R.A.; Kaefer, I.L.; Both, C.; Cechin, S. 2012. Invasive bullfrogs as predators in a Neotropical assemblage: What frog species do they eat? *Animal Biology* 62: 397–408.
- Bonetti, M.F.; Wiens, J.J. 2014. Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133229.
- Borges, R.E.; Santos, L.R. de S.; Benvindo-Souza, M.; Modesto, R.S.; Assis, R.A.; de Oliveira, C. 2019. Genotoxic evaluation in tadpoles associated with agriculture in the Central Cerrado, Brazil. *Archives of environmental contamination and toxicology* 77: 22–28.
- Boyd, I.L.; Freer-Smith, P.H.; Gilligan, C.A.; Godfray, H.C.J. 2013. The consequence of tree pests and diseases for ecosystem services. *Science* 342: 1235773.
- Brown, C.J.; Bode, M.; Venter, O.; Barnes, M.D.; McGowan, J.; Runge, C.A.; et al. 2015. Effective conservation requires clear objectives and prioritizing actions, not places or species. *Proceedings of the National Academy of Sciences* 112: E4342–E4342.
- Brum, F.T.; Graham, C.H.; Costa, G.C.; Hedges, S.B.; Penone, C.; Radeloff, V.C.; et al. 2017. Global priorities for conservation across multiple dimensions of mammalian diversity. *Proceedings of the National Academy of Sciences* 114: 7641–7646.
- Burke, K.L. 2012. Niche contraction of American chestnut in response to chestnut blight. *Canadian Journal of Forest Research* 42: 614–620.
- Burnham, K.P.; Anderson, D.R. 1998. Practical Use of the Information-Theoretic Approach. In: Burnham, K.P.; Anderson, D.R. (Eds.), *Model Selection and Inference: A Practical Information-Theoretic Approach*, Springer, New York, NY, p.75–117.
- Callaghan, C.T.; Liu, G.; Mitchell, B.A.; Poore, A.G.B.; Rowley, J.J.L. 2021. Urbanization negatively impacts frog diversity at continental, regional, and local scales. *Basic and Applied Ecology* 54: 64–74.
- Cardinale, B.J.; Duffy, J.E.; Gonzalez, A.; Hooper, D.U.; Perrings, C.; Venail, P.; et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486: 59–67.
- Carrasco, G.H.; de Souza, M.B.; de Souza Santos, L.R. 2021. Effect of multiple stressors and population decline of frogs. *Environmental Science and Pollution Research* 28: 59519–59527.
- Carvalho, T.; Becker, C.G.; Toledo, L.F. 2017. Historical amphibian declines and extinctions in Brazil linked to chytridiomycosis. *Proceedings of the Royal Society B: Biological Sciences* 284: 20162254.
- Ceballos, G.; García, A.; Ehrlich, P.R. 2010. The sixth extinction crisis: Loss of animal populations and species. *Journal of Cosmology* 8: 31.
- Ceballos, G.; Ehrlich, P.R.; Dirzo, R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the national academy of sciences* 114: E6089–E6096.
- Ceballos, G.; Ehrlich, P.R.; Raven, P.H. 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences* 117: 13596–13602.
- Colwell, R.K.; Brehm, G.; Cardelús, C.L.; Gilman, A.C.; Longino, J.T. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322: 258–261.

- Concepción, E.D.; Obrist, M.K.; Moretti, M.; Altermatt, F.; Baur, B.; Nobis, M.P. 2016. Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. *Urban Ecosystems* 19: 225–242.
- Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological conservation* 128: 231–240.
- Cutler, D.R.; Edwards Jr, T.C.; Beard, K.H.; Cutler, A.; Hess, K.T.; Gibson, J.; et al. 2007. Random forests for classification in ecology. *Ecology* 88: 2783–2792.
- Da Silva, E.T.; Ribeiro Filho, O.P.; Feio, R.N. 2011. Predation of native anurans by invasive bullfrogs in southeastern Brazil: spatial variation and effect of microhabitat use by prey. *South American Journal of Herpetology* 6: 1–10.
- Daszak, P.; Strieby, A.; Cunningham, A.A.; Longcore, J.E.; Brown, C.C.; Porter, D. 2004a. Experimental evidence that the bullfrog (*Rana catesbeiana*) is a potential carrier of chytridiomycosis, an emerging fungal disease of amphibians. *Herpetological Journal* 14: 201–208.
- Daszak, P.; Strieby, A.; Cunningham, A.A.; Longcore, J.E.; Brown, C.C.; Porter, D. 2004b. Experimental evidence that the bullfrog (*Rana catesbeiana*) is a potential carrier of chytridiomycosis, an emerging fungal disease of amphibians. *Herpetological Journal* 14: 201–208.
- Daufresne, M.; Lengfellner, K.; Sommer, U. 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* 106: 12788–12793.
- Dirzo, R.; Young, H.S.; Galetti, M.; Ceballos, G.; Isaac, N.J.; Collen, B. 2014. Defaunation in the Anthropocene. *Science* 345: 401–406.
- Doddington, B.J.; Bosch, J.; Oliver, J.A.; Grassly, N.C.; Garcia, G.; Schmidt, B.R.; et al. 2013. Context-dependent amphibian host population response to an invading pathogen. *Ecology* 94: 1795–1804.
- Doherty, T.S.; Glen, A.S.; Nimmo, D.G.; Ritchie, E.G.; Dickman, C.R. 2016. Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences* 113: 11261–11265.
- Etard, A.; Pigot, A.L.; Newbold, T. 2022. Intensive human land uses negatively affect vertebrate functional diversity. *Ecology Letters* 25: 330–343.
- Evans, K.L.; Gaston, K.J. 2005. People, energy and avian species richness. *Global Ecology and Biogeography* 14: 187–196.
- Faith, D.P. 1992. Conservation evaluation and phylogenetic diversity. *Biological conservation* 61: 1–10.
- Ficetola, G.F.; Thuiller, W.; Miaud, C. 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. *Diversity and distributions* 13: 476–485.
- Fick, S.E.; Hijmans, R.J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International journal of climatology* 37: 4302–4315.
- Fotheringham, A.S.; Brunson, C.; Charlton, M. 2003. *Geographically weighted regression: the analysis of spatially varying relationships*. John Wiley & Sons, .
- Gallardo, B.; Zieritz, A.; Aldridge, D.C. 2015. The Importance of the Human Footprint in Shaping the Global Distribution of Terrestrial, Freshwater and Marine Invaders. *PLOS ONE* 10: e0125801.
- Garner, T.W.; Perkins, M.W.; Govindarajulu, P.; Seglie, D.; Walker, S.; Cunningham, A.A.; et al. 2006. The emerging amphibian pathogen *Batrachochytrium dendrobatidis* globally infects introduced populations of the North American bullfrog, *Rana catesbeiana*. *Biology letters* 2: 455–459.
- Gaston, K.J. 2005. Biodiversity and extinction: species and people. *Progress in Physical Geography* 29: 239–247.

- Giovanelli, J.G.; Haddad, C.F.; Alexandrino, J. 2008. Predicting the potential distribution of the alien invasive American bullfrog (*Lithobates catesbeianus*) in Brazil. *Biological Invasions* 10: 585–590.
- Gomez-Mestre, I.; Pyron, R.A.; Wiens, J.J. 2012. Phylogenetic Analyses Reveal Unexpected Patterns in the Evolution of Reproductive Modes in Frogs. *Evolution* 66: 3687–3700.
- Gonçalves, F.; Sales, L.P.; Galetti, M.; Pires, M.M. 2021. Combined impacts of climate and land use change and the future restructuring of Neotropical bat biodiversity. *Perspectives in Ecology and Conservation* 19: 454–463.
- Grant, E.H.C.; Miller, D.A.W.; Schmidt, B.R.; Adams, M.J.; Amburgey, S.M.; Chambert, T.; et al. 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Scientific Reports* 6.
- Guisan, A.; Edwards Jr, T.C.; Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological modelling* 157: 89–100.
- Guo, F.; Bonebrake, T.C.; Gibson, L. 2019. Land-Use Change Alters Host and Vector Communities and May Elevate Disease Risk. *EcoHealth* 16: 647–658.
- Haddad, C.F.; Toledo, L.F.; Prado, C.P.; Loebmann, D.; Gasparini, J.L.; Sazima, I. 2013. *Guia dos anfíbios da Mata Atlântica: diversidade e biologia*. Anolis Books, .
- Halliday, F.W.; Rohr, J.R. 2019. Measuring the shape of the biodiversity-disease relationship across systems reveals new findings and key gaps. *Nature communications* 10: 5032.
- Hamer, A.J.; McDonnell, M.J. 2008a. Amphibian ecology and conservation in the urbanising world: a review. *Biological conservation* 141: 2432–2449.
- Hamer, A.J.; McDonnell, M.J. 2008b. Amphibian ecology and conservation in the urbanising world: a review. *Biological conservation* 141: 2432–2449.
- Hamer, A.J.; Parris, K.M. 2011. Local and landscape determinants of amphibian communities in urban ponds. *Ecological Applications* 21: 378–390.
- Heo, J.-H.; Lee, H.-J.; Kim, I.-H.; Fong, J.J.; Kim, J.-K.; Jeong, S.; et al. 2014. Can an Invasive Prey Species Induce Morphological and Behavioral Changes in an Endemic Predator? Evidence from a South Korean Snake (*Oocatochus rufodorsatus*). *Asian Herpetological Research* 5: 245–254.
- Hijmans, R.J.; Phillips, S.; Leathwick, J.; Elith, J. 2017. dismo: Species distribution modeling. *R package version* 1: 1–1.
- Hof, C.; Araújo, M.B.; Jetz, W.; Rahbek, C. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480: 516–519.
- Holt, R.D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659–19665.
- Homola, J.J.; Loftin, C.S.; Kinnison, M.T. 2019. Landscape genetics reveals unique and shared effects of urbanization for two sympatric pool-breeding amphibians. *Ecology and Evolution* 9: 11799–11823.
- Hunke, P.; Mueller, E.N.; Schröder, B.; Zeilhofer, P. 2015. The Brazilian Cerrado: assessment of water and soil degradation in catchments under intensive agricultural use. *Ecohydrology* 8: 1154–1180.
- IUNC. 2022. *The IUCN Red List of Threatened Species*. IUCN Red List of Threatened Species. (<https://www.iucnredlist.org/en>). Accessed on 21 Jun. 2022.
- Ives, A.R.; Midford, P.E.; Garland, T., Jr. 2007. Within-Species Variation and Measurement Error in Phylogenetic Comparative Methods. *Systematic Biology* 56: 252–270.
- James, T.Y.; Toledo, L.F.; Rödder, D.; da Silva Leite, D.; Belasen, A.M.; Betancourt-Román, C.M.; et al. 2015. Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: lessons from the first 15 years of amphibian chytridiomycosis research. *Ecology and Evolution* 5: 4079–4097.

- Jancowski, K.; Orchard, S. 2013. Stomach contents from invasive American bullfrogs *Rana catesbeiana* (= *Lithobates catesbeianus*) on southern Vancouver Island, British Columbia, Canada. *NeoBiota* 16: 17.
- Jenkins, C.N.; Pimm, S.L.; Joppa, L.N. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences* 110.
- Jetz, W.; Pyron, R.A. 2018a. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature ecology & evolution* 2: 850.
- Jetz, W.; Pyron, R.A. 2018b. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature ecology & evolution* 2: 850.
- Kafash, A.; Ashrafi, S.; Ohler, A.; Yousefi, M.; Malakoutikhah, S.; Koehler, G.; et al. 2018. Climate change produces winners and losers: Differential responses of amphibians in mountain forests of the Near East. *Global Ecology and Conservation* 16: e00471.
- Kats, L.B.; Ferrer, R.P. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Diversity and distributions* 9: 99–110.
- Keesing, F.; Belden, L.K.; Daszak, P.; Dobson, A.; Harvell, C.D.; Holt, R.D.; et al. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468: 647–652.
- Keil, P.; Storch, D.; Jetz, W. 2015. On the decline of biodiversity due to area loss. *Nature communications* 6: 1–11.
- Kenis, M.; Auger-Rozenberg, M.-A.; Roques, A.; Timms, L.; Péré, C.; Cock, M.J.; et al. 2009. Ecological effects of invasive alien insects. *Biological Invasions* 11: 21–45.
- Kirch, P.V.; Hartshorn, A.S.; Chadwick, O.A.; Vitousek, P.M.; Sherrod, D.R.; Coil, J.; et al. 2004. Environment, agriculture, and settlement patterns in a marginal Polynesian landscape. *Proceedings of the National Academy of Sciences* 101: 9936–9941.
- Knapp, S.; Winter, M.; Klotz, S. 2017. Increasing species richness but decreasing phylogenetic richness and divergence over a 320-year period of urbanization. *Journal of Applied Ecology* 54: 1152–1160.
- Kraus, F. 2008. *Alien reptiles and amphibians: a scientific compendium and analysis*. Vol. 4. Springer Science & Business Media, .
- Kraus, F. 2015. Impacts from invasive reptiles and amphibians. *Annual Review of Ecology, Evolution, and Systematics* 46: 75–97.
- Laliberté, E.; Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.
- Lawler, J.J.; Shafer, S.L.; Bancroft, B.A.; Blaustein, A.R. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. *Conservation Biology* 24: 38–50.
- Leivas, P.T.; Leivas, F.W.; Moura, M.O. 2012. Diet and trophic niche of *Lithobates catesbeianus* (Amphibia: Anura). *Zoologia (Curitiba)* 29: 405–412.
- Lenth, R.; Singmann, H.; Love, J.; Buerkner, P.; Herve, M. 2019. Package ‘emmeans.’ .
- Li, Y.; Cohen, J.M.; Rohr, J.R. 2013. Review and synthesis of the effects of climate change on amphibians. *Integrative Zoology* 8: 145–161.
- Li, Y.; Ke, Z.; Wang, Y.; Blackburn, T.M. 2011. Frog community responses to recent American bullfrog invasions. *Current Zoology* 57: 83–92.
- Lion, M.B.; Mazzochini, G.G.; Garda, A.A.; Lee, T.M.; Bickford, D.; Costa, G.C.; et al. 2019. Global patterns of terrestriality in amphibian reproduction. *Global Ecology and Biogeography* 28: 744–756.
- Lips, K.R. 2016. Overview of chytrid emergence and impacts on amphibians. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150465.
- Lips, K.R.; Diffendorfer, J.; Mendelson III, J.R.; Sears, M.W. 2008. Riding the wave: reconciling the roles of disease and climate change in amphibian declines. *PLoS biology* 6: e72.

- Lips, K.R.; Brem, F.; Brenes, R.; Reeve, J.D.; Alford, R.A.; Voyles, J.; et al. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences* 103: 3165–3170.
- Liu, X.; Rohr, J.R.; Li, Y. 2013. Climate, vegetation, introduced hosts and trade shape a global wildlife pandemic. *Proceedings of the Royal Society B: Biological Sciences* 280: 20122506.
- Liu, X.; Li, M.; Sun, Y.; Deng, X. 2010. Support vector data description for weed/corn image recognition. *Journal of Food, Agriculture and Environment* 8: 214–219.
- Löwenberg-Neto, P. 2014. Neotropical region: a shapefile of Morrone's (2014) biogeographical regionalisation. *Zootaxa* 3802: 0.
- Luck, G.W. 2007. A review of the relationships between human population density and biodiversity. *Biological Reviews* 82: 607–645.
- Mac Nally, R.; Horrocks, G.; Lada, H.; Lake, P.S.; Thomson, J.R.; Taylor, A.C. 2009. Distribution of anuran amphibians in massively altered landscapes in south-eastern Australia: effects of climate change in an aridifying region. *Global Ecology and Biogeography* 18: 575–585.
- Martínez-Freiría, F.; Tarroso, P.; Rebelo, H.; Brito, J.C. 2016. Contemporary niche contraction affects climate change predictions for elephants and giraffes. *Diversity and distributions* 22: 432–444.
- McCullagh, P.; Nelder, J.A. 2019. *Generalized linear models*. Routledge, .
- McDonnell, M.J.; Hahs, A.K. 2015. Adaptation and adaptedness of organisms to urban environments. *Annual review of ecology, evolution, and systematics* 46: 261–280.
- Medeiros, C.I.; Both, C.; Grant, T.; Hartz, S.M. 2017. Invasion of the acoustic niche: variable responses by native species to invasive American bullfrog calls. *Biological Invasions* 19: 675–690.
- Menéndez-Guerrero, P.A.; Graham, C.H. 2013. Evaluating multiple causes of amphibian declines of Ecuador using geographical quantitative analyses. *Ecography* 36: 756–769.
- Miller, D.A.W.; Grant, E.H.C.; Muths, E.; Amburgey, S.M.; Adams, M.J.; Joseph, M.B.; et al. 2018. Quantifying climate sensitivity and climate-driven change in North American amphibian communities. *Nature Communications* 9: 3926.
- Mittermeier, R.A.; Turner, W.R.; Larsen, F.W.; Brooks, T.M.; Gascon, C. 2011a. Global Biodiversity Conservation: The Critical Role of Hotspots. In: Zachos, F.E.; Habel, J.C. (Eds.), *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas*, Springer, Berlin, Heidelberg, p.3–22.
- Mittermeier, R.A.; Turner, W.R.; Larsen, F.W.; Brooks, T.M.; Gascon, C. 2011b. Global biodiversity conservation: the critical role of hotspots. In: *Biodiversity Hotspots*, Springer, p.3–22.
- Monzón, J.; Moyer-Horner, L.; Palamar, M.B. 2011. Climate change and species range dynamics in protected areas. *Bioscience* 61: 752–761.
- Morrone, J.J. 2014. Biogeographical regionalisation of the Neotropical region. *Zootaxa* 3782: 1.
- Mumme, S.; Jochum, M.; Brose, U.; Haneda, N.F.; Barnes, A.D. 2015. Functional diversity and stability of litter-invertebrate communities following land-use change in Sumatra, Indonesia. *Biological Conservation* 191: 750–758.
- Ndriantsoa, S.H.; Riemann, J.C.; Raminosoa, N.; Rödel, M.-O.; Glos, J.S. 2017. Amphibian diversity in the matrix of a fragmented landscape around Ranomafana in Madagascar depends on matrix quality. *Tropical Conservation Science* 10: 1940082916686065.
- Nock, C.A.; Paquette, A.; Follett, M.; Nowak, D.J.; Messier, C. 2013. Effects of urbanization on tree species functional diversity in eastern North America. *Ecosystems* 16: 1487–1497.
- Nopper, J.; Lauströer, B.; Rödel, M.-O.; Ganzhorn, J.U. 2017. A structurally enriched agricultural landscape maintains high reptile diversity in sub-arid south-western Madagascar. *Journal of Applied Ecology* 54: 480–488.
- Nori, J.; Urbina-Cardona, J.N.; Loyola, R.D.; Lescano, J.N.; Leynaud, G.C. 2011. Climate Change and American Bullfrog Invasion: What Could We Expect in South America? *PLoS ONE* 6: e25718.

- Nowakowski, A.J.; Thompson, M.E.; Donnelly, M.A.; Todd, B.D. 2017. Amphibian sensitivity to habitat modification is associated with population trends and species traits. *Global Ecology and Biogeography* 26: 700–712.
- Nowakowski, A.J.; Frishkoff, L.O.; Thompson, M.E.; Smith, T.M.; Todd, B.D. 2018. Phylogenetic homogenization of amphibian assemblages in human-altered habitats across the globe. *Proceedings of the National Academy of Sciences* 115: E3454–E3462.
- Oda, F.H.; Guerra, V.; Grou, E.; de Lima, L.D.; Proença, H.C.; Gambale, P.G.; et al. 2019. Native anuran species as prey of invasive American Bullfrog, *Lithobates catesbeianus*, in Brazil: a review with new predation records. *Amphib. Reptile Conserv.* 13.
- O’hanlon, S.J.; Rieux, A.; Farrer, R.A.; Rosa, G.M.; Waldman, B.; Bataille, A.; et al. 2018. Recent Asian origin of chytrid fungi causing global amphibian declines. *Science* 360: 621–627.
- O’Hanlon, S.J.; Rieux, A.; Farrer, R.A.; Rosa, G.M.; Waldman, B.; Bataille, A.; et al. 2018. Recent Asian origin of chytrid fungi causing global amphibian declines. *Science* 360: 621–627.
- Olalla-Tárraga, M.Á.; Rodríguez, M.Á. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann’s rule, urodeles its converse. *Global Ecology and Biogeography* 16: 606–617.
- Oliveira, B.F.; Scheffers, B.R. 2019. Vertical stratification influences global patterns of biodiversity. *Ecography* 42: 249–249.
- Oliveira, B.F.; São-Pedro, V.A.; Santos-Barrera, G.; Penone, C.; Costa, G.C. 2017. AmphiBIO, a global database for amphibian ecological traits. *Scientific data* 4: 170123.
- de Oliveira Roque, F.; Menezes, J.F.; Northfield, T.; Ochoa-Quintero, J.M.; Campbell, M.J.; Laurance, W.F. 2018. Warning signals of biodiversity collapse across gradients of tropical forest loss. *Scientific Reports* 8: 1–7.
- Olson, D.H.; Aanensen, D.M.; Ronnenberg, K.L.; Powell, C.I.; Walker, S.F.; Bielby, J.; et al. 2013. Mapping the global emergence of *Batrachochytrium dendrobatidis*, the amphibian chytrid fungus. *PloS one* 8: e56802.
- Pereira, H.M.; Navarro, L.M.; Martins, I.S. 2012. Global Biodiversity Change: The Bad, the Good, and the Unknown. *Annual Review of Environment and Resources* 37: 25–50.
- Petchey, O.L.; Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology letters* 5: 402–411.
- Petchey, O.L.; Gaston, K.J. 2006. Functional diversity: back to basics and looking forward. *Ecology letters* 9: 741–758.
- Peters, R.H. 1983. *The Ecological Implications of Body Size*. In: *Cambridge Studies in Ecology*. Cambridge University Press, Cambridge, .
- Phillips, S. 2017. Maxnet: Fitting ‘maxent’ species distribution models with ‘glmnet.’ *R package version 0.1 2*.
- Phillips, S.J.; Anderson, R.P.; Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological modelling* 190: 231–259.
- Pili, A.N.; Supsup, C.E.; Sy, E.Y.; Diesmos, M.L.L.; Diesmos, A.C. 2019. Spatial dynamics of invasion and distribution of alien frogs in a biodiversity hotspot archipelago. *Island invasives: scaling up to meet the challenge*: 337–347.
- Pimm, S.L.; Jenkins, C.N.; Abell, R.; Brooks, T.M.; Gittleman, J.L.; Joppa, L.N.; et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344: 1246752.
- Pincheira-Donoso, D.; Harvey, L.P.; Guirguis, J.; Goodyear, L.E.; Finn, C.; Johnson, J.; et al. 2022. Temporal and spatial patterns of vertebrate extinctions during the Anthropocene. *BioRxiv*.
- Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D.; Heisterkamp, S.; Van Willigen, B.; et al. 2017. Package ‘nlme.’ *Linear and nonlinear mixed effects models, version 3*.
- Purvis, A.; Agapow, P.-M.; Gittleman, J.L.; Mace, G.M. 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288: 328–330.

- Puschendorf, R.; Hoskin, C.J.; Cashins, S.D.; McDONALD, K.; Skerratt, L.F.; Vanderwal, J.; et al. 2011. Environmental refuge from disease-driven amphibian extinction. *Conservation Biology* 25: 956–964.
- Pyšek, P.; Hulme, P.E.; Simberloff, D.; Bacher, S.; Blackburn, T.M.; Carlton, J.T.; et al. 2020. Scientists' warning on invasive alien species. *Biological Reviews* 95: 1511–1534.
- R Core Team, R.D.C. 2021. R: A language and environment for statistical computing. *R foundation for statistical computing, Vienna, Austria*.
- Rachowicz, L.J.; Vredenburg, V.T. 2004. Transmission of *Batrachochytrium dendrobatidis* within and between amphibian life stages. *Diseases of aquatic organisms* 61: 75–83.
- Rago, A.; While, G.M.; Uller, T. 2012. Introduction pathway and climate trump ecology and life history as predictors of establishment success in alien frogs and toads. *Ecology and evolution* 2: 1437–1445.
- Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in ecology and evolution* 3: 217–223.
- Riemann, J.C.; Ndriantsoa, S.H.; Rödel, M.-O.; Glos, J. 2017. Functional diversity in a fragmented landscape — Habitat alterations affect functional trait composition of frog assemblages in Madagascar. *Global Ecology and Conservation* 10: 173–183.
- Rogalski, M.A.; Gowler, C.D.; Shaw, C.L.; Hufbauer, R.A.; Duffy, M.A. 2017. Human drivers of ecological and evolutionary dynamics in emerging and disappearing infectious disease systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160043.
- Rohr, J.R.; Civitello, D.J.; Halliday, F.W.; Hudson, P.J.; Lafferty, K.D.; Wood, C.L.; et al. 2020. Towards common ground in the biodiversity–disease debate. *Nature ecology & evolution* 4: 24–33.
- Ron, S.R.; Duellman, W.E.; Coloma, L.A.; Bustamante, M.R. 2003. Population decline of the Jambato toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador. *Journal of Herpetology*: 116–126.
- Rosenblum, E.B.; Voyles, J.; Poorten, T.J.; Stajich, J.E. 2010. The deadly chytrid fungus: a story of an emerging pathogen. *PLoS Pathogens* 6: e1000550.
- Rowley, J.J.; Alford, R.A. 2013. Hot bodies protect amphibians against chytrid infection in nature. *Scientific reports* 3: 1515.
- Royle, J.A.; Chandler, R.B.; Yackulic, C.; Nichols, J.D. 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution* 3: 545–554.
- Scheele, B.; Pasmans, F.; Skerratt, L.; Berger, L.; Martel, A.; Beukema, W.; et al. 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* 363: 1459–1463.
- Schiesari, L.; Grillitsch, B.; Grillitsch, H. 2007. Biogeographic Biases in Research and Their Consequences for Linking Amphibian Declines to Pollution. *Conservation Biology* 21: 465–471.
- Schivo, F.; Bauni, V.; Krug, P.; Quintana, R.D. 2019. Distribution and richness of amphibians under different climate change scenarios in a subtropical region of South America. *Applied Geography* 103: 70–89.
- Schloegel, L.M.; Ferreira, C.M.; James, T.Y.; Hipolito, M.; Longcore, J.E.; Hyatt, A.D.; et al. 2010. The North American bullfrog as a reservoir for the spread of *Batrachochytrium dendrobatidis* in Brazil. *Animal Conservation* 13: 53–61.
- Searle, C.L.; Biga, L.M.; Spatafora, J.W.; Blaustein, A.R. 2011. A dilution effect in the emerging amphibian pathogen *Batrachochytrium dendrobatidis*. *Proceedings of the National Academy of Sciences* 108: 16322–16326.
- Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. *The journal of wildlife management*: 615–631.

- Semlitsch, R.D.; Skelly, D.K. 2008. Ecology and conservation of pool-breeding amphibians. *Science and conservation of vernal pools in northeastern North America*. CRC Press, Boca Raton, FL: 127–148.
- Sievers, M.; Parris, K.M.; Swearer, S.E.; Hale, R. 2018. Stormwater wetlands can function as ecological traps for urban frogs. *Ecological Applications* 28: 1106–1115.
- da Silva, F.R.; Almeida-Neto, M.; do Prado, V.H.M.; Haddad, C.F.B.; de Cerqueira Rossa-Feres, D. 2012. Humidity levels drive reproductive modes and phylogenetic diversity of amphibians in the Brazilian Atlantic Forest. *Journal of Biogeography* 39: 1720–1732.
- Smith, K.G.; Lips, K.R.; Chase, J.M. 2009. Selecting for extinction: nonrandom disease-associated extinction homogenizes amphibian biotas. *Ecology Letters* 12: 1069–1078.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology letters* 10: 1115–1123.
- Staude, I.R.; Navarro, L.M.; Pereira, H.M. 2020. Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography* 29: 16–25.
- Strubbe, D.; Broennimann, O.; Chiron, F.; Matthysen, E. 2013. Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. *Global Ecology and Biogeography* 22: 962–970.
- Tennekes, M. 2018. tmap: Thematic Maps in R. *Journal of Statistical Software* 84: 1–39.
- Toledo, L.F.; Ribeiro, R.S.; Haddad, C.F. 2007. Anurans as prey: an exploratory analysis and size relationships between predators and their prey. *Journal of Zoology* 271: 170–177.
- Trimble, M.J.; van Aarde, R.J. 2014. Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemism. *Animal Conservation* 17: 441–453.
- Tucker, C.M.; Cadotte, M.W.; Carvalho, S.B.; Davies, T.J.; Ferrier, S.; Fritz, S.A.; et al. 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* 92: 698–715.
- Tylianakis, J.M.; Didham, R.K.; Bascompte, J.; Wardle, D.A. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology letters* 11: 1351–1363.
- Urban, M.C. 2015. Accelerating extinction risk from climate change. *Science* 348: 571–573.
- Urbina, J.; Bredeweg, E.M.; Garcia, T.S.; Blaustein, A.R. 2018. Host–pathogen dynamics among the invasive American bullfrog (*Lithobates catesbeianus*) and chytrid fungus (*Batrachochytrium dendrobatidis*). *Hydrobiologia* 817: 267–277.
- Van Rooij, P.; Martel, A.; Haesebrouck, F.; Pasmans, F. 2015. Amphibian chytridiomycosis: a review with focus on fungus-host interactions. *Veterinary research* 46: 1–22.
- Venesky, M.D.; Liu, X.; Sauer, E.L.; Rohr, J.R. 2014a. Linking manipulative experiments to field data to test the dilution effect. *Journal of Animal Ecology* 83: 557–565.
- Venesky, M.D.; Raffel, T.R.; McMahon, T.A.; Rohr, J.R. 2014b. Confronting inconsistencies in the amphibian-chytridiomycosis system: Implications for disease management. *Biological Reviews* 89: 477–483.
- Venter, O.; Sanderson, E.W.; Magrath, A.; Allan, J.R.; Beher, J.; Jones, K.R.; et al. 2016a. Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific data* 3: 1–10.
- Venter, O.; Sanderson, E.W.; Magrath, A.; Allan, J.R.; Beher, J.; Jones, K.R.; et al. 2016b. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications* 7: 12558.
- Vilela, B.; Villalobos, F. 2015. letsR: a new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution* 6: 1229–1234.
- Villéger, S.; Mason, N.W.H.; Mouillot, D. 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *Ecology* 89: 2290–2301.
- Vitousek, P.M.; Ladefoged, T.N.; Kirch, P.V.; Hartshorn, A.S.; Graves, M.W.; Hotchkiss, S.C.; et al. 2004. Soils, agriculture, and society in precontact Hawaii. *Science* 304: 1665–1669.

- Voyles, J.; Young, S.; Berger, L.; Campbell, C.; Voyles, W.F.; Dinudom, A.; et al. 2009. Pathogenesis of chytridiomycosis, a cause of catastrophic amphibian declines. *Science* 326: 582–585.
- Wang, Y.; Guo, Z.; Pearl, C.A.; Li, Y. 2007. Body size affects the predatory interactions between introduced American Bullfrogs (*Rana catesbeiana*) and native anurans in China: an experimental study. *Journal of Herpetology* 41: 514–520.
- Warren, D.L.; Glor, R.E.; Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution: International Journal of Organic Evolution* 62: 2868–2883.
- Warren, D.L.; Glor, R.E.; Turelli, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33: 607–611.
- Webb, C.O.; Ackerly, D.D.; McPeck, M.A.; Donoghue, M.J. 2002. Phylogenies and community ecology. *Annual review of ecology and systematics* 33: 475–505.
- Weir, I.S.; Pettitt, A.N. 2000. Binary probability maps using a hidden conditional autoregressive Gaussian process with an application to Finnish common toad data. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 49: 473–484.
- Westgate, M.J.; Scheele, B.C.; Ikin, K.; Hoefer, A.M.; Beaty, R.M.; Evans, M.; et al. 2015. Citizen Science Program Shows Urban Areas Have Lower Occurrence of Frog Species, but Not Accelerated Declines. *PLOS ONE* 10: e0140973.
- Wheeler, D.C.; Páez, A. 2009. Geographically weighted regression. In: *Handbook of Applied Spatial Analysis: Software Tools, Methods and Applications*, Springer, p.461–486.
- Wilk, A.J.; Donlon, K.C.; Peterman, W.E. 2020. Effects of habitat fragment size and isolation on the density and genetics of urban red-backed salamanders (*Plethodon cinereus*). *Urban Ecosystems* 23: 761–773.
- Winter, M.; Devictor, V.; Schweiger, O. 2013. Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution* 28: 199–204.
- Xie, G.Y.; Olson, D.H.; Blaustein, A.R. 2016. Projecting the Global Distribution of the Emerging Amphibian Fungal Pathogen, *Batrachochytrium dendrobatidis*, Based on IPCC Climate Futures. *PLOS ONE* 11: e0160746.
- Yang, L.; Zhao, S.; Liu, S. 2022. A global analysis of urbanization effects on amphibian richness: Patterns and drivers. *Global Environmental Change* 73: 102476.
- Yap, T.A.; Koo, M.S.; Ambrose, R.F.; Vredenburg, V.T. 2018a. Introduced bullfrog facilitates pathogen invasion in the western United States. *PloS one* 13: e0188384.
- Yap, T.A.; Koo, M.S.; Ambrose, R.F.; Vredenburg, V.T. 2018b. Introduced bullfrog facilitates pathogen invasion in the western United States. *PLOS ONE* 13: e0188384.
- Young, H.S.; McCauley, D.J.; Galetti, M.; Dirzo, R. 2016. Patterns, causes, and consequences of anthropocene defaunation. *Annual review of ecology, evolution, and systematics* 47: 333–358.
- Zamora-Gutierrez, V.; Pearson, R.G.; Green, R.E.; Jones, K.E. 2018. Forecasting the combined effects of climate and land use change on Mexican bats. *Diversity and Distributions* 24: 363–374.
- Zeileis, A.; Cribari-Neto, F.; Gruen, B.; Kosmidis, I.; Simas, A.B.; Rocha, A.V.; et al. 2016. Package ‘betareg.’ *R package* 3.
- Zipkin, E.F.; DiRenzo, G.V. 2022. Biodiversity is decimated by the cascading effects of the amphibian-killing chytrid fungus. *PLOS Pathogens* 18: e1010624.
- Zizka, A.; Silvestro, D.; Andermann, T.; Azevedo, J.; Duarte Ritter, C.; Edler, D.; et al. 2019. CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* 10: 744–751.
- Zumbado-Ulate, H.; García-Rodríguez, A.; Vredenburg, V.T.; Searle, C. 2019. Infection with *Batrachochytrium dendrobatidis* is common in tropical lowland habitats: Implications for amphibian conservation. *Ecology and evolution* 9: 4917–4930.
- Zuur, A.F.; Ieno, E.N.; Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution* 1: 3–14.

Zuur, A.F.; Ieno, E.N.; Walker, N.J.; Saveliev, A.A.; Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Vol. 574. Springer, .