MARINA LOPES BUENO

BIOLOGICAL INVASIONS IN BRAZILIAN FRESHWATER ECOSYSTEMS: PRESENT SITUATION OF ALIEN FISH SPECIES AND ASSESSMENT OF ENVIRONMENTAL FACTORS AS INVASION DRIVERS

LAVRAS-MG
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Prof. Dr. Rafael Dudeque Zenni
Orientador

Prof. Dr. Paulo dos Santos Pompeu
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INVASÕES BIOLÓGICAS EM ECOSSISTEMAS DULCÍCOLAS BRASILEIROS:
SITUAÇÃO ATUAL DAS ESPÉCIES EXÓTICAS DE PEIXES E AVALIAÇÃO DE FATORES AMBIENTAIS COMO FACILITADORES DE INVASÃO

Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, para a obtenção do título de Doutora.

APROVADA em 10 de dezembro de 2021.

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2021

Á memória de Maria Eugênia e Maria Cristina Godinho Lopes.

Dedico

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Muito obrigada!

"It always seems impossible until it's done." (Nelson Mandela)

RESUMO

As invasões biológicas são uma consequência global de um mundo cada vez mais conectado e impactado pelas ações humanas. A expansão das atividades humanas, como construções de barragens, aquicultura, pesca e urbanização, vem transformando a estrutura, dinâmica e funcionamento dos ambientes dulcícolas e, consequentemente, favorecendo o estabelecimento e invasão de espécies exóticas de peixes. O número de espécies exóticas invasoras tende a aumentar indefinidamente ao longo do tempo, podendo causar inúmeros e severos impactos nos ambientes receptores como, por exemplo, mudanças nos ecossistemas e extinção de espécies nativas. Compreender os aspectos biológicos e ecológicos das espécies introduzidas, bem como identificar quais variáveis do habitat favorecem o estabelecimento destas espécies, são passos importantes para controlar futuras invasões biológicas e manejar aquelas que já aconteceram. Assim, os objetivos deste estudo foram: (I) preparar uma lista atualizada dos peixes introduzidos nas principais bacias do sudeste do Brasil (Alto Paraná, Paraíba do Sul, São Francisco, Jequitinhonha, Doce e Mucuri), informando seus status de invasão, categoria de impacto ambiental (EICAT/IUCN), vias de introdução, origem e atributos taxonômicos; (II) avaliar a importância relativa das variáveis físicas do habitat na presença e abundância do peixe invasor *Poecilia reticulata*, uma espécie amplamente distribuída no Brasil e em regiões tropicais e temperadas do mundo. Os resultados deste trabalho indicaram um crescente número de espécies de peixes introduzidas e estabelecidas nas bacias estudadas, comparado com estudos anteriores. Existem dados detalhados sobre a distribuição e status populacional destas espécies no Brasil, mas há uma carência de estudos ecológicos sobre os impactos de tais introduções. Este estudo também destacou a importância da urbanização no estabelecimento e invasão de *P. reticulata*. As áreas urbanas são vias relevantes para a introdução desta espécie exótica invasora, e as modificações no habitat causadas pela urbanização criam condições ambientais distintas que beneficiam esta espécie, assim como outros invasores oportunistas. Esse resultado reforça a importância da proteção da integridade biótica dos cursos d'água para o gerenciamento e prevenção de invasões biológicas.

Palavras-chave: Ictiofauna, Lista de espécies. Espécies não-nativas. Distúrbios humanos. Água doce.

ABSTRACT

Biological invasions are a global consequence of a world increasingly connected and impacted by human actions. The expansion of human activities, such as construction of dams, aquaculture, fishing and urbanization, has been transforming the structure, dynamics and functioning of freshwater environments and, consequently, favoring the establishment and invasion of alien fish species. The number of invasive alien species tends to increase indefinitely over time, which can cause numerous and severe impacts on recipient environments, such as changes in ecosystems and native species extinction. Understanding the biological and ecological aspects of introduced species, as well as identifying which habitat variables are favorable to the establishment of these species, are important steps to control future biological invasions and manage those that have already taken place. Thus, the aims of this study were: (I) to prepare an updated list of fish introduced in the main watersheds of southeastern Brazil (Upper Paraná, Paraíba do Sul, São Francisco, Jequitinhonha, Doce and Mucuri), informing their invasion status, category of environmental impact (EICAT/IUCN), pathways of introduction, origin and taxonomic attributes; and (II) to evaluate the relative importance of physical habitat variables on the presence and abundance of the invasive fish *Poecilia reticulata*, a species widely distributed in Brazil and in tropical and temperate regions. The results of this work indicated an increasing number of fish species introduced and established in the studied watersheds, compared to previous studies. There were detailed data on the distribution and population status of these species in Brazil, but a lack of ecological studies on the impacts of such introductions. The present study also highlighted the importance of urbanization in the establishment and invasion of *P. reticulata*. Urban areas were relevant pathways for the introduction of this invasive species, and the changes in the habitat caused by urbanization created distinct environmental conditions that benefit this species, as well as other opportunistic invaders. This result reinforces the importance of protecting the biotic integrity of watercourses for the management and prevention of biological invasions.

Keywords: Ichthyofauna, Checklist. Non-native species. Human disturbance. Freshwater.

SUMÁRIO

PRIMEIRA PARTE – INTRODUÇÃO GERAL

Espécies exóticas invasoras causam diversas mudanças ambientais, sendo consideradas uma das principais causas diretas de perda de biodiversidade global (IPBES 2019; PYŠEK et al. 2020). Espécies são consideradas exóticas quando são transportadas para além de seus limites e área geográfica nativa para um local em que elas não possuem distribuição natural (BLACKBURN et al 2011). Este processo é mediado, de maneira voluntária ou involuntária, por ações humanas (LEÃO et al. 2011). O número de espécies exóticas invasoras vem crescendo em todo o mundo devido às altas taxas de introduções por diversas vias e vetores, facilitadas pela globalização e aumento da população humana (SEEBENS et al. 2017; PYŠEK et al. 2020). No entanto, para que o processo de invasão biológica ocorra de fato, as espécies exóticas precisam passar por alguns filtros ambientais, biológicos e impostos pelo homem divididos em cinco estágios: nativo, transporte, introdução, estabelecimento e invasão (BLACKBURN et al. 2011; ZENNI et al. 2017). As primeiras barreiras a serem superadas são a geográfica e o cativeiro e/ou cultivo. Muitas espécies conseguem ultrapassar esses limites geográficos ou os impostos pelo homem, como as cercas dos cativeiros, e são introduzidas em novas áreas. Assim, estas espécies são denominadas exóticas. Se as espécies exóticas conseguirem sobreviver no novo habitat, serão classificadas como casuais ou introduzidas. Se houver reprodução com alta probabilidade de os descendentes sobreviverem, as espécies serão classificadas como naturalizadas ou estabelecidas. Portanto, para que este processo de estabelecimento ocorra, as espécies devem superar as barreiras de sobrevivência e reprodução. Caso as espécies estabelecidas consigam sair de sua área de introdução e expandam suas distribuições, haverá dispersão. Como os ambientes vão se diversificando ao longo do processo de dispersão, as populações precisam superar uma barreira ambiental para que ocorra a invasão. Somente após a superação de todas essas barreiras e estágios é que as espécies passam a ser classificadas como exóticas invasoras (BLACKBURN et al. 2011; LEÃO et al. 2011).

O processo de invasão biológica pode ser influenciado pelas características das espécies (traços de história de vida) e por outros fatores, como a pressão de propágulos, condições do ambiente, traços das comunidades receptoras e interações invasor-comunidade (CATFORD et al. 2019). A pressão de propágulos está relacionada com a frequência e a quantidade de organismos que são introduzidos no ambiente receptor (LOCKWOOD et al. 2005). Assim, quanto mais propágulos em condições satisfatórias forem liberados, maior a chance do sucesso de estabelecimento e invasão (LOCKWOOD et al. 2005, 2009; SIMBERLOFF 2009). No entanto, os organismos precisam se ajustar às novas condições impostas pelo ambiente receptor para se estabelecerem, de modo que a semelhança entre o ambiente de origem e o invadido pode beneficiar o reultado da invasão (GARCIA et al. 2021). A degradação do ambiente causada pelo homem também pode favorecer as invasões biológicas e exacerbar seus impactos por meio de alterações nos habitats e nas interações ecológicas, abrindo assim novos nichos vagos para os invasores mais adaptáveis e tolerantes (GHERARDI 2007; RICCIARDI & MACISAAC 2011). Apesar disso, a maioria das espécies introduzidas não consegue se estabelecer e invadir qualquer ambiente (GARCIA et al. 2021), porém aquelas que obtem sucesso frequentemente causam grandes impactos nos ecossistemas (VITULE et al. 2009).

Os impactos causados pelas invasões biológicas podem ser complexos e, muitas vezes, irreversíveis (BLACKBURN et al. 2014; PYŠEK et al. 2020). As espécies exóticas invasoras podem causar mudanças substanciais nos ecossistemas receptores (BLACKBURN et al. 2014; JESCHKE et al. 2014; MENDOZA & KOLLEF 2014), e consequentemente, podem alterar seus processos (CUCHEROUSSET & OLDEN 2011, VILÀ et al. 2011; KATSANEVAKIS et al. 2014; PYŠEK et al. 2020), ameaçar a biodiversidade nativa (VITULE et al. 2009, CUCHEROUSSET & OLDEN 2011, JESCHKE et al. 2014; ROSA et al. 2017), provocar prejuízos econômicos (ADELINO et al. 2021; HAUBROCK et al. 2021; HERINGER et al. 2021) e de saúde pública (NÚÑEZ et al. 2020; VILÀ et al. 2021). Estes impactos tendem a aumentar com o tempo em todos os tipos de habitat, mas são especialmente maiores nas ilhas e nos ambientes dulcícolas (IPBES 2019). Peixes exóticos invasores, por exemplo, têm causado impactos ecológicos e econômicos danosos nos ecossistemas aquáticos e na sociedade humana (HAUBROCK et al. 2021), mas muitos desses impactos ainda não são bem compreendidos tanto no meio científico, quanto pela população em geral (JESCHKE et al. 2014; COURCHAMP et al. 2017; BUENO et al. 2021).

Apesar do número crescente de trabalhos sobre invasões biológicas (REICHARD & WHITE 2003; HEGER et al. 2021), ainda existem lacunas de conhecimento que devem ser preenchidas. Além da falta de informação concreta sobre os reais impactos ambientais que as espécies podem causar nos ecossistemas receptores (BUENO et al. 2021), dados sobre as taxas de sucesso de invasão por espécie e por ambiente podem ser difíceis de serem obtidos, devido à maioria das introduções serem realizadas de forma clandestina (GARCIA et al.

2021). Também existem lacunas nos dados disponíveis sobre os impactos econômicos das invasões biológicas, indicando subestimação e a necessidade de aprimoração dos relatórios de custos (HAUBROCK et al. 2021; RENAULT et al. 2021). Na América do Sul e África, por exemplo, não existem relatos sobre prejuízos econômicos causados por espécies exóticas invasoras de peixes (HAUBROCK et al. 2021). Nesse sentido, as invasões biológicas devem receber mais atenção, e maiores esforços devem ser realizados para o preenchimento de lacunas desta área, possibilitando uma transferência de conhecimento entre ciência e gestão (FOXCROFT et al. 2020). Por outro lado, informações sobre a distribuição das espécies exóticas invasoras estão disponíveis em artigos científicos e vários bancos de dados (PYŠEK et al. 2020), como GRIIS (Global Register of Introduced and Invasive Species), CABI (Invasive Species Compendium), DIAS (Database on Introductions of Aquatic Species – FAO) e Base de Dados Nacional de Espécies Exóticas Invasoras. Através destas informações, um bom conhecimento foi gerado sobre o número de espécies exóticas estabelecidas e invasoras em várias regiões e ecossistemas (PYŠEK et al. 2020). No entanto, em um país como o Brasil, que possui extensas áreas e inúmeras bacias hidrográficas, ainda há dificuldades na obtenção destas informações sobre as espécies de peixes introduzidas (GARCIA et al. 2021), destacando a importância de novos inventários e listas de espécies exóticas.

Dado o cenário de aumento alarmante das invasões biológicas e degradação em ambientes dulcícolas, o objetivo geral deste trabalho foi avaliar a atual situação das espécies de peixes introduzidas em importantes bacias hidrográficas do Brasil, bem como avaliar como o habitat físico pode beneficiar estas invasões. A partir da compreensão destas questões, espera-se fornecer uma base para um maior conhecimento sobre o processo de invasão em ambientes dulcícolas, possibilitando a implementação de programas de manejo efetivos e de prevenção de futuras introduções.

REFERÊNCIAS

ADELINO, J.R.P.; HERINGER, G.; DIAGNE, C.; COURCHAMP, F.; FARIA, L.D.B.; ZENNI, R.D. The economic costs of biological invasions in Brazil: a first assessment. In: Zenni, R.D.; McDermott, S.; García-Berthou, E.; Essl, F. (Eds.) The economic costs of biological invasions around the world. **NeoBiota** v. 67, p. 349-374, 2021. DOI: 10.3897/neobiota.67.59185

BLACKBURN T.M.; PYŠEK, P.; BACHER, S.; CARLTON, J.T.; DUNCAN, R.P.; JAROSIK, V.; WILSON, J.R.U.; RICHARDSON, D.M.A. A proposed unified framework for biological invasions. **Trends in Ecology & Evolution**, v. 26, p. 333–339, 2011.

BLACKBURN, T.M.; ESSL, F.; EVANS, T. et al. A unified classification of alien species based on the magnitude of their environmental impacts. **PLoS Biol**, v. 12, e1001850, 2014.

BUENO, M.L.; MAGALHÃES, A.L.B.; ANDRADE NETO, F.R.; ALVES, C.B.M.; ROSA, D.M.; JUNQUEIRA, N.T.; PESSALI, T.C.; POMPEU, P.S.; ZENNI, R.D. Alien fish fauna of southeastern Brazil: species status, introduction pathways, distribution and impacts. **Biol Invasions**, 2021. DOI: 10.1007/s10530-021-02564-x

CATFORD, J.A.; SMITH, A.L.; WRAGG, P.D.; CLARK, A.T.; KOSMALA, M.; CAVENDER-BARES, J.; REICH, P.B.; TILMAN, D. Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. **Ecology Letters**, v. 22, n. 4, p. 593–604, 2019. DOI:10.1111/ele.13220

COURCHAMP, F.; FOURNIER, A.; BELLARD, C.; BERTELSMEIER, C.; BONNAUD, E.; JESCHKE, J.M.; RUSSELL, J.C. Invasion Biology: Specific Problems and Possible Solutions. **Trends in Ecology & Evolution**, v. 32, n. 1, 2017. DOI: 10.1016/j.tree.2016.11.001

CUCHEROUSSET, J.; OLDEN, J.D. Ecological Impacts of Non-native Freshwater Fishes. **Fisheries**, v. 36, n. 5, 2011.

FOXCROFT, L.C.; VAN WILGEN, B.W.; ABRAHAMS, B.; ESLER, K.J.; WANNENBURGH, A. Knowing-doing continuum or knowing-doing gap? Information flow between researchers and managers of biological invasions in South Africa. In: Van Wilgen B.W.; Measey J.; Richardson D.M.; Wilson J.R.U.; Zengeya T.A. (Eds.) **Biological Invasions in South Africa**, pp. 831–853, 2020. Springer, Berlin.

GARCIA, D.A.Z.; PELICICE, F.M.; DE BRITO, M.F.G; ORSI, M.L.; MAGALHÃES, A.L.B. Peixes não-nativos em riachos no brasil: estado da arte, lacunas de conhecimento e perspectivas. **Oecologia Australis**, v. 25, n. 2, p. 565-587, 2021. DOI: 10.4257/oeco.2021.2502.21

GHERARDI, F. Biological invasions in inland waters: an overview. In: GHERARDI, F (Ed.) Biological invaders in inland waters: Profiles, distribution, and threats. Invading Nature - Springer Series In: **Invasion Ecology**, vol 2. Springer, Dordrecht. 2007. DOI: 10.1007/978-1-4020-6029-8_1

HAUBROCK, P.J.; BERNERY, C.; CUTHBERT, R.N.; et al. Knowledge gaps in economic costs of invasive alien fish worldwide. **Science of the Total Environment**, v. 803, 149875, 2021. DOI: 10.1016/j.scitotenv.2021.1498

HEGER, T.; JESCHKE, J.M.; KOLLMANN, J. Some reflections on current invasion science and perspectives for an exciting future. **NeoBiota**, v. 68, p. 79-100. DOI: 10.3897/neobiota.68.68997

HERINGER, G.; ANGULO, E.; BALLESTEROS-MEJIA, L.; CAPINHA, C.; COURCHAMP, F.; DIAGNE, C.; DUBOSCQ-CARRA, V.G.; NÚÑEZ, M.A.; ZENNI, R.D. The economic costs of biological invasions in Central and South America: a first regional assessment. In: Zenni, R.D.; McDermott, S.; García-Berthou, E.; Essl, F. (Eds.) The economic costs of biological invasions around the world. **NeoBiota**, v. 67, p. 401–426, 2021. DOI: 10.3897/neobiota.67.59193

IPBES. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. Brondizio, J. Settele, S. Díaz, H. T. Ngo (Eds.). **IPBES** secretariat, Bonn, Germany, p. 1148, 2019. DOI: 10.5281/zenodo.3831673

JESCHKE, J.M.; BACHER, S.; BLACKBURN, T.M.; DICK, J.T.; ESSL, F.; EVANS, T.; GAERTNER, M.; HULME, P.E.; KÜHN, I.; MRUGAŁA, A.; PERGL, J.; PYŠEK, P.; RABITSCH, W.; RICCIARDI, A.; RICHARDSON, D.M.; SENDEK, A.; VILÀ, M.; WINTER, M.; KUMSCHICK, S. Defining the Impact of Non-Native Species. **Conservation Biology**, v. 28, p. 1188-1194, 2014. DOI: 10.1111/cobi.12299

KATSANEVAKIS, S.; WALLENTINUS, I.; ZENETOS, A.; LEPPÄKOSKI, E.; ÇINAR, M.E.; OZTÜRK, B.; GRABOWSKI, M.; GOLANI, D.; CARDOSO, A.C. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan- European review. **Aquatic Invasions**, Helsinki, v. 9, n. 4, p. 391- 423, 2014

LEÃO, T.C.C.; ALMEIDA, W.R.; DECHOUM, M.; ZILLER, S.R. Espécies Exóticas Invasoras no Nordeste do Brasil: Contextualização, Manejo e Políticas Públicas. Recife: Cepan, 2011.

LOCKWOOD, J.L.; CASSEY, P.; BLACKBURN, T. The role of propagule pressure in explaining species invasions. **Trends in Ecology and Evolution**, v. 20, p. 223-228, 2005.

LOCKWOOD, J.L.; HOOPES, M.F.; MARCHETTI, M.P. **Invasion Ecology**. Oxford: Blackwell Publishing, 304 p., 2007.

MENDOZA, R.; KOLEFF, P. Introducción de especies exóticas acuáticas en México y en el mundo. In: Mendoza, R.; Koleff, P. (Eds.). **Especies acuáticas invasoras en México**. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, p. 17-41, 2014.

MILLENNIUM ECOSYSTEM ASSESSMENT. Ecosystems and Human Well-being: Biodiversity Synthesis. Washington, DC, 2005.

NÚÑEZ, M.A.; PAUCHARD, A.; RICCIARDI, A. Invasion Science and the Global Spread of SARS-CoV-2. **Trends in Ecology & Evolution**, 2020. DOI: 10.1016/j.tree.2020.05.004

PYŠEK, P.; HULME, P.E.; SIMBERLOFF, D.; et al. Scientists' warning on invasive alien species. **Biol Rev**, v. 95, p. 1511-1534, 2020. DOI: 10.1111/brv.12627

REICHARD, S.; WHITE, P.S. Invasion Biology: an emerging field of study. **Ann Missouri Bot Gard**, v. 90, p. 64–66, 2003. DOI: 10.2307/3298526

RENAULT, D.; MANFRINI, E.; LEROY, B.; DIAGNE, C.; BALLESTEROS-MEJIA, L.; ANGULO, E.; COURCHAMP, F. Biological invasions in France: Alarming costs and even more alarming knowledge gaps. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds.) The economic costs of biological invasions around the world. **NeoBiota**, v. 67, p. 191-224, 2021. DOI: 10.3897/neobiota.67.59134

RICCIARDI, A.; MACISAAC, H.J. Impacts of Biological Invasions on Freshwater Ecosystems. In: Richardson DM (Ed.) **Fifty Years of Invasion Ecology**, 2011. DOI: 10.1002/9781444329988.ch16

ROSA, C.A.; CURI, N.H.A.; PUERTAS, F.; PASSAMANI, M. Alien terrestrial mammals in Brazil: status and management. **Biol Invasions**, v. 19, 2101, 2017. DOI: 10.1007/s10530-017-1423-3

SEEBENS, H.; BLACKBURN, T.M.; DYER, E.E.; et al. No saturation in the accumulation of alien species in the worldwide. **Nature Communications**, v. 8, 14435, 2017.

SIMBERLOFF, D. The role of propagule pressure in biological invasions. **Annu Rev Ecol Evol Syst**, v. 40, p. 81–102, 2009.

VILÀ, M.; DUNN, A.M.; ESSL, F.; GÓMEZ-DÍAZ, E.; HULME, P.E.; JESCHKE, J.M.; NÚÑEZ, M.A.; OSTFELD, R.S.; PAUCHARD, A.; RICCIARDI, A.; GALLARDO, B. Viewing Emerging Human Infectious Epidemics through the Lens of Invasion Biology. **BioScience**, v. 71, n. 7, p. 722-740, 2021. DOI: 10.1093/biosci/biab047

VILÀ, M.; ESPINAR, J.L.; HEJDA, M.; HULME, P.E.; JAROŠÍK, V.; MARON, J.L.; PERGL, J.; SCHAFFNER, U.; SUN, Y.; PYŠEK, P. Ecological impacts of invasive alien plants: a metaanalysis of their effects on species, communities and ecosystems. **Ecology Letters**, Montpellier, v. 14, n. 7, p. 702-708, 2011.

VITULE, J.R.S.; FREIRE, C.A.; SIMBERLOFF, D. Introduction of non-native freshwater fish can certainly be bad. **Fish and Fisheries**, v. 10, p. 98-108, 2009.

ZENNI, R.D.; DICKIE, I.A.; WINGFIELD, M.J.; HIRSCH, H.; CROUS, C.J.; MEYERSON, L.A.; BURGESS, T.I.; ZIMMERMANN, T.G.; KLOCK, M.M.; SIEMANN, E.; ERFMEIER, A.; ARAGON, R.; MONTTI, L.; LE ROUX, J.J. Evolutionary dynamics of tree invasions: complementing the unified framework for biological invasions. **AoB PLANTS** v. 9, plw085, 2017. DOI: 10.1093/aobpla/plw085

SEGUNDA PARTE – ARTIGOS*

ARTIGO I

Alien fish fauna of southeastern Brazil: species status, introduction pathways, distribution and impacts

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Alien fish fauna of southeastern Brazil: species status, introduction pathways, distribution and impacts

Abstract

Compiled inventories with information on the distribution, status and impacts of invasive alien species are essential for the study, management and monitoring of biological invasions. Despite their great importance, such studies are lacking for alien freshwater fish species in Brazil. Therefore, our aim was to improve the knowledge of the regional richness of alien species, leading to the closing of existing regional data gaps. We performed extensive bibliographic research and consulted with experts to update the list of freshwater alien fishes of six watersheds in southeastern Brazil (Upper Paraná, Paraíba do Sul, São Francisco, Mucuri, Jequitinhonha and Doce), and provided information on species invasion status, environmental impact category, pathway of introduction, origin and species taxonomic attributes. We compiled a list of 201 alien fish species introduced in the six watersheds (to 2019) through six pathways: aquarium trade, geographical barrier breach (after the flooding of a natural barrier by the construction of a hydroelectric power plant), aquaculture, stocking for sport fishing, live bait and biological control. The invasion status of the species varied among watersheds, and it was possible to characterize the impact of only 11 species. Our results show there are detailed data on the distribution and population status of alien fishes in Brazil, but also a lack of ecological studies on the impacts of such introductions. Research on the impacts of alien fish species on recipient ecosystems are urgently needed owing to the present high number and wide distribution of invasive species and lack of knowledge on the consequences of these invasions.

Keywords Checklist, non-native species, ichthyofauna, freshwater, invasion status, invasive species

Resumo

Inventários compilados com informações sobre a distribuição, status e impactos das espécies exóticas invasoras são essenciais para o estudo, manejo e monitoramento de invasões biológicas. Apesar da grande importância, tais estudos são escassos para espécies exóticas de peixes de água doce no Brasil. Portanto, nosso objetivo foi aprimorar o conhecimento da riqueza regional de espécies exóticas, visando a diminuição das lacunas de dados regionais existentes. Realizamos uma extensa pesquisa bibliográfica e consultamos pesquisadores especializados para atualizar a lista de peixes exóticos de seis bacias hidrográficas no sudeste do Brasil (Alto Paraná, Paraíba do Sul, São Francisco, Mucuri, Jequitinhonha e Doce), adicionando informações sobre o status de invasão das espécies, categoria de impacto ambiental, vias de introdução, origem e atributos taxonômicos das espécies. Compilamos uma lista com 201 espécies exóticas de peixes introduzidas nas seis bacias hidrográficas (até 2019) por seis vias: comércio de peixes ornamentais, quebra de barreira geográfica (após o alagamento de uma barreira natural pela construção de uma usina hidrelétrica), aquicultura, estocagem para pesca, isca viva e controle biológico. Os status de invasão das espécies variaram entre as bacias hidrográficas e foi possível categorizar o impacto de apenas 11 espécies. Nossos resultados mostram que existem dados detalhados sobre a distribuição e status populacional de peixes exóticos no Brasil, mas também há uma carência de estudos ecológicos sobre os impactos de tais introduções. Pesquisas sobre os impactos de espécies exóticas de peixes nos ambientes receptores são urgentemente necessárias devido ao alto número e disseminação de espécies invasoras e à falta de conhecimento sobre as consequências dessas invasões.

Palavras-chave: Lista de espécies, espécies não-nativas, ictiofauna, água doce, status de invasão, espécies invasoras

Introduction

Invasive alien species can cause changes in recipient ecosystems (Blackburn et al. 2014; Jeschke et al. 2014; Mendoza and Kollef 2014) and, consequently, can alter ecological processes (Cucherousset and Olden 2011; Katsanevakis et al. 2014; Ricciardi et al. 2017), threaten native biodiversity (Vitule et al. 2009; Jeschke et al. 2014; Ricciardi et al. 2017) and cause socioeconomic and public health problems (Ricciardi et al. 2017; Lima-Junior et al. 2018). The deliberate introduction of freshwater alien fishes is a historical practice that has become common worldwide since the end of the 1800s (Welcomme 1988; Padilla and Williams 2004; Mandrak and Cudmore 2010, Pelicice et al. 2017). Fishes have been transported and introduced outside their native ranges for many reasons, including aquaculture, aquarium trade, biological control, stocking, sport fishing and bait (Alves et al. 2007; Pelicice et al. 2017; Vitule et al. 2019). Despite being a great threat to native freshwater fishes (Vitule et al. 2009), the rate of alien fish introduction has been increasing rapidly in South America, including Brazil (Lima-Junior et al. 2018; Magalhães et al. 2019; Vitule et al. 2019 and references therein).

Fish introductions started in the early 20th century in Brazil, when escapes from reservoir stocking programs resulted in the establishment of many alien species in rivers (Gurgel and Oliveira 1987; Alves et al. 2007; Brito et al. 2020). By the mid-20th century, fish introductions occurred mainly due to the production and release of alien species by hydroelectric power companies that invested in the development of fish production technology to minimize the impacts of their dams to migratory species (Alves et al. 2007; Pelicice et al. 2017; Lima-Junior et al. 2018). During this period, there was a significant removal of a geographic barrier in southeastern Brazil (Upper Paraná River basin) that resulted in massive fish introductions after the construction of Itaipu Hydroelectric Power Plant (Júlio-Júnior et al. 2009; Vitule et al. 2012). More recently, in the early 21st century, fish production for the aquarium trade has stimulated the transport of fish species (mostly from the Amazon region) to new watersheds within Brazil (Alves et al. 2007; Vitule et al. 2019; Magalhães et al. 2019, 2020). Aquaculture and fish stocking also played a significant role throughout the 20th and early 21st century (Pelicice et al. 2017; Lima-Junior et al. 2018; Nobile et al. 2019; Magalhães et al. 2020).

There are many studies on biological invasions in freshwater environments in Brazil (e.g. Júlio-Júnior et al. 2009; Britton and Orsi 2012; Magalhães and Jacobi 2013a; Sales et al. 2018; Magalhães et al. 2019), but comprehensive reviews of the invasion status of alien fishes, their distribution and impacts are lacking, despite being essential for the study, monitoring and management of biological invasions (Latombe et al. 2016). Species inventories are very important for testing theories on the distributions, causes, and consequences of biological invasions (Olden 2006; Pyšek et al. 2018). The knowledge about regional fauna and floras obtained from these inventories and databases may be used in macroecological analyses in order to provide insights into the invasion process dynamics (Dawson et al. 2017; Vinogradova et al. 2018; Pyšek et al. 2018, 2019; Vitule et al. 2019). For southeastern Brazil, the most invaded region in the country, the last published compiled inventory comprising more than one watershed was a state list of freshwater alien fishes published by Alves et al. (2007).

The southeastern region is the most populous and economically developed in Brazil (IBGE 2020); consequently, it suffers many anthropogenic impacts, and its watersheds are highly impacted by the introduction of alien species, construction of hydroelectric plants, land-use changes, and sewage pollution (Agostinho et al. 2008; Martins 2008; Andrade 2010; Pompeu 2010; Vieira 2010; Fernandes et al. 2016; Carvalho et al. 2017). Commercial (e.g. fish farming) and ornamental (e.g. aquarium trade) aquaculture is a common practice in southeastern Brazil (Britton and Orsi 2012; Magalhães and Jacobi 2013). Furthermore, the largest center of ornamental fish farming in South America is located in this region, resulting in a high number of species established due to aquarium dumping (Alves et al. 2007; Pelicice et al. 2017; Lima-Junior et al. 2018; Nobile et al. 2019; Magalhães et al. 2017, 2020).

The objective of our study was to prepare an updated comprehensive list of freshwater alien fishes established in the main watersheds in the southeastern region of Brazil. Information was compiled on fish species invasion status (casual, naturalized, invasive), categories of environmental impact (massive, major, moderate, minor, minimal, deficient data, no alien populations, not evaluated), pathways of introduction, origin and taxonomic attributes (family and order). Based on this information, the main research questions investigated for the study region were: i) what alien fish species are introduced?; ii) does the compiled information vary among the studied watersheds?; and, iii) do origin and pathways influence alien species distributions? By improving our knowledge of the alien species in the study region, we provide basis for improving the management of alien fish species and preventing future introductions (Pelicice et al. 2017; Pyšek et al. 2018; Vitule et al. 2019).

Methods

Study region

Our study comprised six watersheds draining from the southeast of Brazil to different freshwater ecoregions (numbers following the ecoregion refer to Abell et al. 2008): Ecoregion Northeastern Mata Atlântica (328), including Doce, Jequitinhonha and Mucuri basins; Ecoregion Paraíba do Sul (329); Ecoregion São Francisco (327); and, Ecoregion Upper Paraná (344) (Fig. 1). The data were collected only for the states of southeastern Brazil (Minas Gerais, São Paulo, Rio de Janeiro, and Espírito Santo). This region has an area of approximately 924,565 km² and is one of the most economically developed and anthropogenically impacted regions of Brazil (Pelicice et al. 2017; IBGE 2020). Consequently, these watersheds suffer from stressors such as introduction of alien species, construction of hydroelectric plants, land-use changes, and sewage pollution (Agostinho et al. 2008; Martins 2008; Andrade 2010; Pompeu 2010; Vieira 2010; Fernandes et al. 2016; Carvalho et al. 2017).

The Upper Paraná basin has a total area of approximately 900,000 km² and its southeastern portion drains the states of Minas Gerais and São Paulo. This river basin is situated upstream of Sete Quedas Falls, an ancient natural barrier flooded by the construction of the Itaipu Hydroelectric Power Plant, which allowed the spread of several species from Lower Paraná to Upper Paraná (Langeani et al. 2007; Júlio-Júnior et al. 2009; Pelicice et al. 2017). The São Francisco River basin has approximately 645,000 km², and its source is located in the state of Minas Gerais (Godinho and Godinho 2003; Kohler 2003; Silva et al. 2003). About 37% of its area is located in Minas Gerais, covering the entire portion of the Upper and part of the Middle São Francisco basin (Godinho and Godinho 2003). The Jequitinhonha and Mucuri River basins are located in the southeast and northeast of Brazil, with more than 94% of each basin within the southeast region (Pompeu 2010; Cemig 2019a, b). The Jequitinhonha area is 70,315 km² and drains the states of Minas Gerais and Bahia (Cemig 2019a). The Mucuri basin is smaller and drains an area of 15,400 km², passing through the states of Minas Gerais, Espírito Santo and Bahia (Cemig 2019b). The Doce River basin, 83,400 km², is entirely within the southeast region, draining the states of Minas Gerais and Espírito Santo (Cemig 2019c). The Paraíba do Sul River basin is also located entirely in the southeast region, in the states of Minas Gerais, São Paulo and Rio de Janeiro (Vieira and Rodrigues 2010), draining an area of approximately 57,000 km² (Cemig 2019d). This river basin is located in one of the largest urban-industrial centers in Brazil and, consequently, it is impacted by several anthropogenic actions (Teixeira et al. 2005; Vieira and Rodrigues 2010). The largest center of ornamental fish farming in South America is in this river basin, especially in the region of the municipality of Muriaé (Vieira and Rodrigues 2010; Magalhães and Jacobi 2013a; Magalhães et al. 2019). The center provides more than 70% of the Brazilian demand for aquarium fishes (Magalhães and Jacobi 2017).

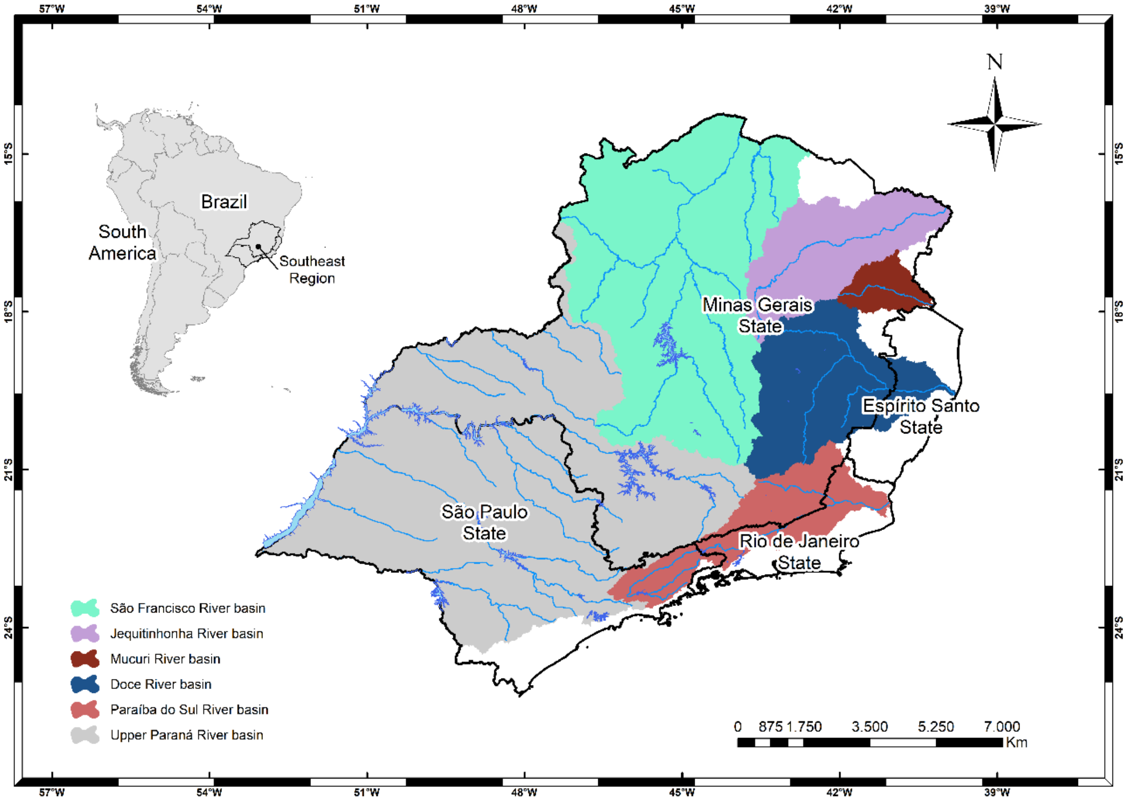

Fig. 1 Watersheds of southeastern Brazil included in this study.

Lists of alien fish species and their attributes

An updated list of fish species introduced in southeastern Brazil was compiled based on extensive bibliographic searches, empirical knowledge of experts (academics and private consultants in environmental projects in the region) and unpublished records (see Electronic Appendix S1 for data sources). For this, we had the support of alien fish experts who contributed and validated the data in a workshop at the Universidade Federal de Lavras (UFLA), July 9 – 10, 2018. The list contains information on species invasion status: casual (individuals that survive in the location where they were introduced, but do not reproduce), naturalized (individuals that survive, reproduce, and have a self-sustaining population) or invasive (species that have survived, spread, and are reproducing at multiple sites) (Blackburn et al. 2011); impacts on recipient environments (based on the EICAT scheme; see Blackburn et al. 2014); pathways of introduction; the region of native distribution (termed ‘origin’: Africa, Asia, Central America, North America, South America, and Europe); and taxonomic order and family.

Searches were conducted in Google Scholar (https://scholar.google.com), Web of Science (https://mjl.clarivate.com) and Fish Base (www.fishbase.org – Froese and Pauly 2019) and included books and journal articles/manuscripts published up to 2019. We used combinations of the following search terms, in English and Portuguese: “fish species”, “ichthyofauna”, “alien”, “non-native”, “introduced”, “Doce River”, “Jequitinhonha River”, “Mucuri River”, “Paraíba do Sul River”, “São Francisco River” and “Upper Paraná River”. Each expert also contributed publications and personal data collected in field surveys.

The invasion status of each species was defined according to Blackburn et al. (2011), and the impacts (massive, major, moderate, minor, minimal, deficient data, no alien populations, not evaluated) caused by them were categorized according to Blackburn et al. (2014) and the Environmental Impact Classification of Alien Taxa (EICAT / IUCN) (IUCN 2020). For the EICAT classification, there must be strong evidence of the impacts caused by alien species in the recipient environments. For example, when there is evidence that a species leads to the replacement and local extinction of native species and produces irreversible changes in the structure of communities and the abiotic or biotic composition of ecosystems, its impact is classified as massive (Blackburn et al. 2014). However, if the environmental impact caused by the species is reversible, its impact is classified as major. For a species to be classified as moderate, there must be evidence that it causes declines in the population densities of native species, but no changes to the structure of communities or to the abiotic or biotic composition of ecosystems, and has no impacts that would cause it to be classified in a higher impact category (see all impact categories in Blackburn et al. 2014). The status and impact of each species were categorized for each watershed at the UFLA workshop, based on data collected in the literature and field experience of fish experts.

Origin, taxonomic order and family, and pathways of introduction were compiled/obtained from the literature. The pathways found included aquarium trade (ornamental freshwater fish trade), aquaculture (commercial aquaculture to obtain animal protein), biological control (e.g. introduction of poeciliids to control malaria-vector mosquitoes), sport fishing, live bait and anthropogenic breaching of geographic barriers (e.g. Sete Quedas Falls flooded by the construction of the Itaipu Hydroelectric Power Plant) (Alves et al. 2007; Júlio-Júnior et al. 2009; Britton and Orsi 2012).

The numbers of native species for each watershed were based on literature (Bizerril 1999; Ingenito and Buckup 2007; Langeani et al. 2007; Andrade-Neto 2010; Pompeu 2010; Vieira 2010; Vieira and Rodrigues 2010; Oyakawa and Menezes 2011; Gomes et al. 2015; Pugedo et al. 2016; Barbosa et al. 2017; Reis 2018, Salvador et al. 2018; Econservation 2019; Ribeiro et al. 2019; Fricke et al. 2020) and on unpublished data collected by the authors. These numbers were adjusted to included only the native species that occur in their respective watersheds in the southeastern region of Brazil.

Statistical analysis

To test if observed richness of alien fish species across the six studied watersheds in southeastern Brazil varied significantly by origin, pathway, and family we used χ^2 goodness-of-fit tests. The expected number of alien species in each category for each watershed was the mean number of alien species from all watersheds ($\sum_{i=0}^{n} K/n$), where K is the number of alien species in each category and n is the number of watersheds). In the χ^2 goodness-of-fit test for family, only families with more than one species were used to conform with the assumptions of the test.

A matrix of origin (c) × pathways (r) was built to determine the influence of interacting factors on the distribution of alien fish species. Each cell corresponded to the sum of alien species with both r and c attributes. Pearson's chi-square test of independence was used to explore the relationship of the matrix. All analyses were based on the methods used by Zenni (2014) and were done in R 3.6.1 (R Development Core Team 2019).

Results

The alien fish fauna in the southeastern Brazil watersheds consisted of 201 species, belonging to 16 orders and 48 families. There was an increase from the 104 species introduced throughout Brazil reported by Alves et al. (2007), and compared to other reviews for specific watersheds (e.g. Vieira and Rodrigues 2010; Britton and Orsi 2012; Garcia et al. 2018). The Upper Paraná River basin had a higher number of alien species (n = 116), but Paraíba do Sul had the highest percentage of alien species relative to the regional native species pool (43.0%) (Table 1). The invasion status of species varied among river basins: Upper Paraná, Mucuri, Paraíba do Sul and São Francisco had more casual species; while

Doce and Jequitinhonha had more invasive species. The families that were most represented were Cichlidae (n = 29), Characidae (n = 22), Loricariidae (n = 17), Cyprinidae (n = 11), Pimelodidae (n = 10), Anostomidae (n = 9), Serrasalmidae (n = 9) and Poeciliidae (n = 8). The representation of families significantly differed among regions ($\chi^2 = 182.91$, df = 28, $p < 0.01$; Fig. 2).

Table 1 The numbers of native and alien fish species and invasion status of alien species in each of the watersheds studied in southeastern Brazil.

Watershed	Area (km²)	Native species	Alien species	Invasion status			Proportion of alien species (%)
				casual	naturalized	invasive	
Doce	83,400	114	39	14	10	15	25.5
Jequitinhonha	70,315	68	20	5	6	9	22.7
Mucuri	15,400	47	14	6	3	5	22.9
Paraíba do Sul	57,000	127	96	50	27	19	43.0
São Francisco	645,000	190	39	20	9	10	17.0
Upper Paraná	900,000	265	116	60	21	35	30.4

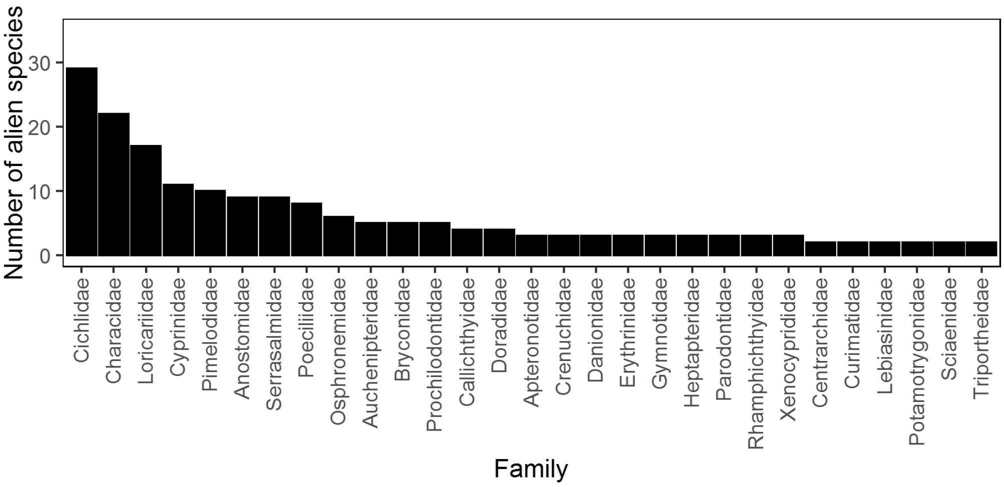

Fig. 2 Number of alien fish species found in the six watersheds in southeastern Brazil, by family.

The numbers of alien fish species of different origins differed significantly across the six watersheds ($\chi^2 = 550.88$, df = 5, $p < 0.01$). Most species originated from South America (n = 159), the figures for other continents were much lower: Asia (n = 26), North America (n = 8), Africa (n = 6), Central America (n = 6) and Europe (n = 1). We found the following six main pathways of introduction of alien fish to southeastern Brazil: aquarium trade (n = 71), geographical barrier breach (n = 58), aquaculture (n = 29), fishing (n = 19), live bait (n = 13) and biological control (n = 5). For 23 species, there was no explicit information on pathway of introduction in the literature. The differences among pathways were statistically significant, with aquarium trade and geographical barrier breach being the most common ($\chi^2 = 117.36$, df = 6, $p < 0.01$). All occurrences of geographic barrier breach were recorded in the Upper Paraná River basin and the majority of aquarium trade records occurred in the Paraíba do Sul River basin (n = 59).

The association between origin and pathway for introduction was significant ($\chi^2 = 81.76$, df = 30, $p < 0.01$; Fig. 3). Most species were introduced from Africa for aquaculture, from Central America and Asia for the aquarium trade, from North America for fishing and aquarium trade, and from South America because of geographical barrier breach, biocontrol and live bait. The number of alien species from the families most represented also differed significantly across pathways, introduced specifically for aquarium trade and aquaculture, and by geographical barrier breach ($\chi^2 = 101.82$, df = 35, $p < 0.01$; Fig. 4).

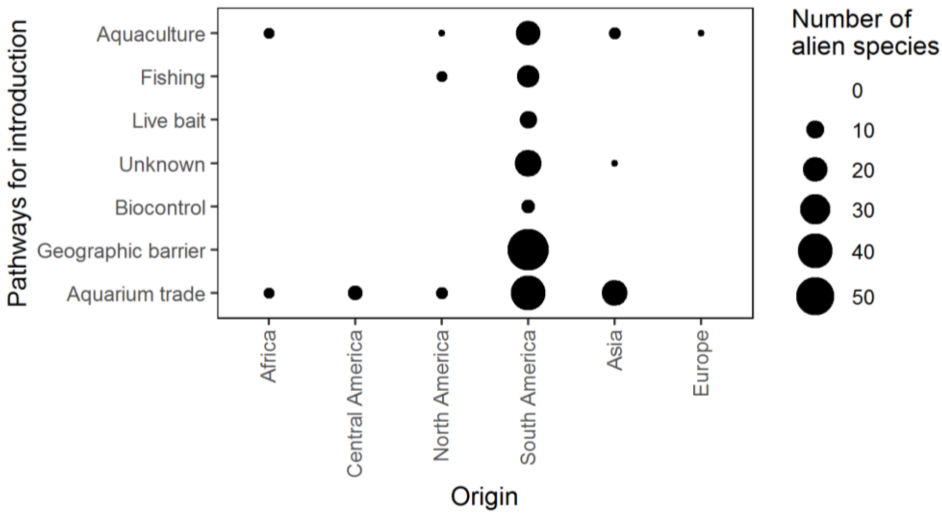

Fig. 3 Interactions of pathways and origin of alien fish species present in southeastern Brazil watersheds.

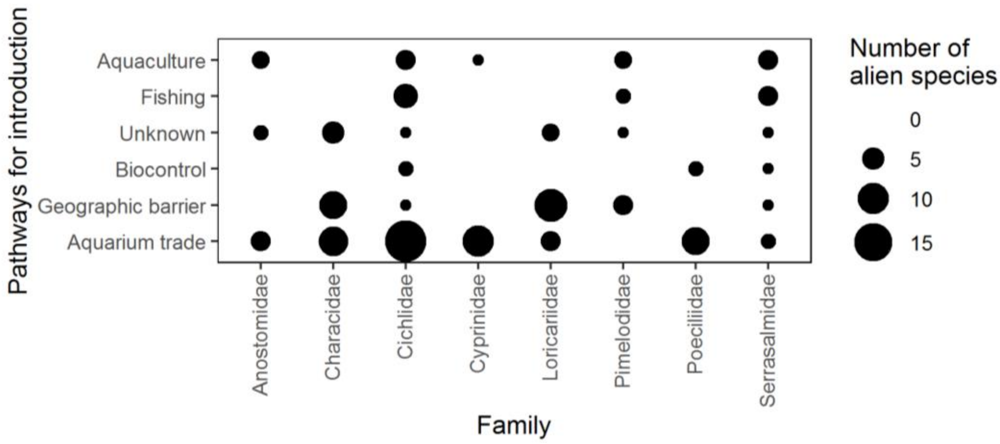

Fig. 4 Interactions of pathways and the most representative taxonomic families of alien fish species present in southeastern.

Regarding the impact categories, we were able to classify only 11 species for which there were available data. *Cichla kelberi* and *Pygocentrus nattereri* were classified as having massive (MV) impact; *Misgurnus anguillicaudatus, Carassius auratus, Pethia conchonius, Danio rerio, and Poecilia sphenops* were classified as having major (MR) impact; *Prochilodus argenteus, P. costatus, Serrasalmus brandtii,* and *S. marginatus* were classified as having moderate (MO) impact (Latini and Petrere 2004; Júlio-Júnior et al. 2009; Pelicice and Agostinho 2009; Kovalenko et al. 2010; Pelicice et al. 2015; Bueno et al. 2016; Fragoso-Moura et al. 2016; Andrade et al. 2018; Sales et al. 2018; Magalhães et al. 2020). Most impact studies on species in the study watersheds only discussed impacts in a speculative manner; therefore, there was insufficient information to classify the remaining 190 species and they were placed in the Data Deficient (DD) category. Species classified as DD* based on expert opinion probably cause damage to the recipient environments, but there are no data regarding their impacts in the study watersheds. Further studies (e.g. field studies) are required to determine the impacts of these species (see Electronic Appendix for the complete list of species and their attributes).

Discussion

The richness of the alien fish fauna of six watersheds in Brazil is greater than previously reported (e.g. Alves et al. 2007, Langeani et al. 2007; Andrade-Neto 2010; Pompeu 2010; Vieira 2010; Vieira and Rodrigues 2010). Most new records were from the Upper Paraná and Paraíba do Sul River basins. The pathways that explain the alien fish community in each river basin also varied, but there was a striking pattern of fish species being transported and released across watersheds within South America (Gubiani et al. 2018; Vitule et al. 2019). Most fishes originated from other watersheds in South America and were introduced mostly via the aquarium trade and as a consequence of geographical barrier breach. The invasion status of fish species varied among watersheds, but four species were invasive in all of them. We classified 11 fish species as having massive, major or moderate impacts; however, most species could not be classified, which reveals an information gap regarding the impacts of most invasive fish species in southeastern Brazil.

The high number of alien fish species in the Upper Paraná River basin can be explained by successful spread from Lower Paraná River basin after construction of the Itaipu Hydroelectric Power Plant, completed in 1982 (Langeani et al. 2007; Júlio-Júnior et al. 2009; Vitule et al. 2012). The filling of the reservoir and the inundation of the Sete Quedas Falls allowed the spread of fish species, which were previously separated by the natural barrier, causing the biotic homogenization of the fish fauna (Júlio-Júnior et al. 2009; Vitule et al. 2012). These species can also disperse, to a lesser degree, through a fish pass built in the Itaipu Dam in 2002 to allow the spawning migration of native species (Makrakis et al. 2007). Thus, it further increases the propagule pressure in the Upper Paraná River and, consequently, increases the probability of alien population establishment (Lockwood et al. 2009; Simberloff 2009; Cassey et al. 2018).

The high number of alien species in the Paraíba do Sul River basin, one of the smallest watersheds in our study, is the result of the high propagule pressure of several pathways that occur in the region. Most of the introductions come from the aquarium trade, especially escapes from Muriaé Ornamental Aquaculture Center ponds (Magalhães and Jacobi 2013a; Magalhães et al. 2019). Most ponds do not have screens on the effluent pipes, which allows ongoing fish escapes into the wild (~ 36,000 release events per year, A.L.B. Magalhães pers. obs.) and, consequently, led to the establishment and spread of several species (Magalhães and Jacobi 2013a and references therein; Magalhães et al. 2019, 2020). In the last 10 years, the aquarium species reared have increased in volume and in number from 60 to more than 200 species (Magalhães et al. 2020). Escape from aquaculture is a global problem that can result in biological invasions, which consequently result in impacts on native ecosystems (FAO 2016; Ju et al. 2019). Nevertheless, many countries do not have strong laws for aquatic biosecurity despite aquaculture being a serious problem (FAO 2016; Patoka et al. 2018; Ju et al. 2019).

Geographical barrier breach and the aquarium trade were the most prevalent pathways of introductions. The notable difference between these two pathways is that the first is like a unique catastrophic event (Júlio-Júnior et al. 2009), but the second is a consequence of recurring introductions (i.e., high propagule pressure) based on the high demand for aquarium species because this geopolitical region is the main center of the aquarium industry in Brazil (*sensu* Magalhães et al. 2017). The latter can be avoided by education (e.g., awareness campaigns to educate people who work at ornamental fish farms), enforcement (releasing alien species, even unintentionally, is an environmental crime according to the National Law on Environmental Crimes 9.605 of 1998 and the Decree 6.514 of 2008), inspection policies, state trade and transportation control (Magalhães et al. 2019).

South America was the main source of alien fish species. The great diversity of native fish fauna in the continent (Reis et al. 2016; Pelicice et al. 2017) enables all types of introduction. Moreover, one of the most significant pathways of introduction was geographical barrier breach that facilitated the spread of many species within the continent. The high number of species from the South American Characidae, Loricariidae and Pimelodidae families is mainly related to high propagule pressure from the introductions in Upper Paraná River. The Serrasalmidae family has many species of interest to commercial fishing and aquaculture, mainly the Amazon species (Jégu 2003; Ribeiro et al. 2014), explaining the high number of serrasalmids introduced in the southeastern watersheds. Species in the Anostomidae family also have high commercial importance - the smaller species for the aquarium trade and larger species for aquaculture (Melo and Röpke 2004; Lima Junior et al. 2018; Nobile et al. 2019).

Asia was an important source of alien fish species, mainly for the aquarium trade. The international aquarium trade is a worldwide hobby that has increased in popularity since the early 1980s (Livengood and Chapman 2011; Teletchea 2016; Magalhães et al. 2017; Lima-Junior et al. 2018). Asian species are known by their potential for the aquarium trade (Ng and Tan 1997), and southeast Asia is a traditional export site for freshwater aquarium fishes (Livengood and Chapman 2011; Ng 2016). Many of these species were introduced to Brazil from aquarium fish farms, mainly in the Paraíba do Sul River basin (Magalhães and Jacobi 2013a; Electronic Appendix). Many of the Asian species belong to the Cyprinidae family, which was one of the most highly represented families in the watersheds studied. Many species in the Cichlidae and Poeciliidae families have been introduced mainly due to aquarium trade as well. Species in these families are commonly kept as ornamental fishes because they are usually colorful, and easy to breed, and have various body shapes and moderate sizes (Kullander 2003; Magalhães and Jacobi 2013b). Consequently, they are very popular in stores and are likely introduced into the wild more frequently and in greater numbers than species in families less common in the aquarium trade (Duggan et al. 2006; Magalhães and Jacobi 2013b). Models for invasion risk of ornamental alien fishes predicted that some species from these three families are potential invaders of rivers in region of Brazil and Australia (Bomford and Glover 2004; Magalhães and Jacobi 2013b).

The invasion status of species varied among watersheds. Many of the species were classified as casual and were the result of escapes from ornamental fish farms (e.g. Paraíba do Sul) and geographical barrier breach (Upper Paraná). If these casual species reproduce and spread into the new habitats, they become potential invaders (Blackburn et al. 2011, Magalhães et al. 2020). Four species were considered invasive in all of watersheds (*Coptodon rendalli*, *Oreochromis niloticus*, *Knodus moenkhausii* and *Poecilia reticulata*). Besides the high propagule pressure, these species are opportunistic and are able to tolerate degraded environments (Casatti et al. 2009; Vitule et al. 2009 and references therein, Carvalho et al. 2017; Carvalho et al. 2019a, Carvalho et al. 2019b), which increases the probability of their establishment and spread.

We were unable to obtain relevant and reliable information regarding the impacts caused by most species, which highlights the knowledge gaps in this area. Of the 11 species for which we had sufficient data, we classified the impacts caused by *Cichla kelberi* and *Pygocentrus nattereri* as massive. The peacock bass, *Cichla kelberi*, is a voracious predatory fish introduced for sport fishing in four of the six basins (Doce, Paraíba do Sul, São Francisco and Upper Paraná), especially in reservoirs and ponds. The introduction of this species has been related to fish community disassembly and the native diversity loss, indicating that this species is a great driver of impacts (Pelicice and Agostinho 2009; Kovalenko et al. 2010; Pelicice et al. 2015). The red piranha, *P. nattereri*, has a predatory behavior (Giacomini et al. 2011) and was introduced for fishing in some Brazilian watersheds (Latini 2016), especially in the lakes of the Middle Doce River (i.e. Rio Doce State Park, state of Minas Gerais), where it was introduced for biological control of other alien fish populations (Latini 2001). Consequently, the abundance of red piranha increased in these lakes over the years, leading to a progressive decrease in the richness and relative abundance of native species and local extinction (Latini 2001; Latini and Petrere 2004; Pinto-Coelho et al. 2008; Bueno el al. 2016; Fragoso-Moura et al. 2016).

Misgurnus anguillicaudatus, *Danio rerio*, *Pethia conchonius*, *Poecilia sphenops*, and *Carassius auratus* were classified as having major impact. The ongoing introduction of these ornamental fishes and associated environmental degradation, in the headwater creeks of Paraíba do Sul River basin in the 2010s, has caused biotic differentiation and the extinction of some native species in the region (Magalhães et al. 2020). The environmental impacts caused by these species are reversible as long as the propagule pressure is stopped and the environments recovered. This can be done by applying sustainable aquaculture principles to reduce escapes from ornamental fish farming facilities (e.g. use of barriers for effluent discharge and the construction of retention ponds) and through habitat restoration activities (Magalhães et al. 2020 and references therein).

The impacts caused by *Prochilodus argenteus*, *P. costatus*, *Serrasalmus brandtii* and *S. marginatus* were classified as moderate. The alien *Prochilodus* species impact the native *P. hartii* in Jequitinhonha River basin, due to genetic introgression (Sales et al. 2018); however, the fundamental ecosystem services provided by Prochilodontidae (Flecker 1996; Winemiller and Jepsen 1998), which may present low functional redundancy even in diverse ecosystems (Taylor et al. 2006), are thought to not be affected. *Serrasalmus brandtii* successfully colonized the Jequitinhonha river after at least two introduction events (Teixeira et al. 2020). One of these events took place in the Irapé hydropower plant reservoir, which *S. brandtii* rapidly colonized. Although the effects of this introduction are evident after years of monitoring the region (e.g. netted fish mutilation increased, *S. brandtii* population growth and dominance), no local extinctions of native species have been observed (Andrade et al. 2018). *Serrasalmus marginatus* was introduced to the Upper Paraná after the construction of the Itaipu Dam. It has become invasive and affected the native species in the region, mainly the native congener *S. maculatus* (Júlio-Júnior et al. 2009). There was an increase in the invasive population to the detriment of native populations in areas affected by Itaipu Dam and in the Upper Paraná floodplain (Agostinho and Júlio-Júnior 2002).

In summary, there has been an increase in the number of alien fish species in southeastern Brazil watersheds compared to previous studies. Efforts to prevent future introductions in these river basins should be undertaken, because once species were established, it is almost impossible to eradicate them (Vitule et al. 2009). Although there are some normative approaches to control or prevent introductions in Brazil (e.g., National Law on Environmental Crimes 9.605 of 1998, Decree 6.514 of 2008), they are not effective (Azevedo-Santos et al. 2015). Conversely, the cultivation of alien fish species is supported for economic reasons, potentially threatening biological diversity and ecosystem services (Pelicice et al. 2014; Brito et al. 2018; Garcia et al. 2018 and references therein). Better education of all stakeholders in all pathways would result in a better-informed society that, in turn, would result in better management of alien fish species (Azevedo-Santos et al. 2015; Magalhães et al. 2019). Enforcement carried out by officials of the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) is also important in order to prevent escapes/releasing based on the National Law of Wildlife Protection 5.197 of 1967. Furthermore, it is essential to assess the risk of biological invasions (e.g. species and pathway risk assessments) in freshwater environmental impact studies, mainly in dam constructions (Júlio-Júnior et al. 2009; Daga et al. 2015).

This study highlights the necessity of more effective efforts in collecting data about the impacts that alien fish species have on recipient ecosystems. Such studies are very important for better communication among scientific community, managers and population, enabling the implementation of effective management programs (Simberloff et al. 2013; Jeschke et al. 2014; Courchamp et al. 2017; N'Guyen et al. 2018; Vitule et al. 2019; Magalhães et al. 2020).

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References

Abell R, Thieme ML, Revenga C, et al. (2008) Freshwater Ecoregions of the World: a new map of biogeographic units for freshwater biodiversity conservation. Bioscience 58:402–414. https://doi.org/10.1641/B580507

Agostinho AA, Pelicice FM, Gomes LC (2008) Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz J Biol 68 (4): 1119-32

Agostinho CS, Júlio-Júnior HF (2002) Observation of an invasion of the piranha *Serrasalmus marginatus* Valenciennes, 1847 (Osteichthyes, Serrasalmidae) into the upper Paraná River, Brazil. Acta Scientiarum, Biol Sci 24 (2): 391-395

Alves CBM, Vieira F, Magalhães ALB, Brito MFG (2007) Impacts of non-native fish species in Minas Gerais, Brazil: present situation and prospects. In: Bert TM (ed) Ecological and Genetic Implications of Aquaculture Activities. 291–314

Andrade FR (2010) Estado atual do conhecimento sobre a fauna de peixes da bacia do Jequitinhonha. MG. Biota 2 (5): 22-35

Andrade FR, Silva LD, Guedes I, Santos AM, Pompeu PS (2018) Non-native white piranhas graze preferentially on caudal fins from large netted fishes. Mar Freshw Res. https://doi.org/10.1071/MF18202

Azevedo-Santos VM, Pelicice FM, Lima-Junior DP, Magalhães ALB, Orsi ML, Vitule JRS, Agostinho AA (2015) How to avoid fish introductions in Brazil: education and information as alternatives. Braz J of Nat Conserv 13: 123-132

Barbosa JM, Soares EC, Cintra IHA, Hermann M, Araújo ARR (2017) Perfil da ictiofauna da bacia do rio São Francisco. Acta Fish Aquat Res 5 (1): 70-90

Bizerril CRSF (1999) A Ictiofauna da Bacia do Rio Paraíba do Sul. Biodiversidade e Padrões Biogeográficos. Braz Arch Biol Technol 42 (2)

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarosík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26: 333-339

Blackburn TM, Essl F, Evans T et al. (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol 12 (5): e1001850

Bomford M, Glover J (2004) Risk assessment model for the import and keeping of exotic freshwater and estuarine finfish. Canberra, Bureau of Rural Sciences

Brito MFG, Daga VS, Vitule JRS (2020) Fisheries and biotic homogenization of freshwater fish in the Brazilian semiarid region. Hydrobiologia. 10.1007/s10750-020-04236-8

Brito MFG, Magalhães ALB, Lima-Junior DP, Pelicice FM, Azevedo-Santos VM, Garcia DAZ, Cunico AM, Vitule JRS (2018) Brazil naturalizes non-native species. Science. 361 (6398): 139

Britton JR, Orsi ML (2012) Non-native fish in aquaculture and sport fishing in Brazil: economic benefits versus risks to fish diversity in the upper River Paraná Basin. Rev Fish Biol Fisheries, 22: 555-565

Bueno ML, Carvalho JC, Rosa DM, Andrade FR, Pompeu PS (2016) Reavaliação da composição e abundância da ictiofauna após décadas da introdução de piscívoros na lagoa dom helvécio, Parque Estadual do Rio Doce, MG. MG. Biota 9 (1): 30-38

Carvalho DR, Castro DMP, Callisto M, Chaves AJM., Moreira MZ, Pompeu PS (2019a) Stable isotopes and stomach content analyses indicate omnivorous habits and opportunistic feeding behavior of an invasive fish. Aquat Ecol 53 (3): 365-381. doi:10.1007/s10452-019-09695-3

Carvalho DR, Flecker AS, Alves CBM, Sparks J, Pompeu PS (2019b) Trophic responses to aquatic pollution of native and exotic livebearer fishes. Sci Total Environ. doi:10.1016/j.scitotenv.2019.05.092

Carvalho DR, Leal CG, Junqueira NT, Castro MA, Fagundes DC, Alves CBM, Hughes R, Pompeu PS (2017) A fish-based multimetric index for Brazilian savanna streams. Ecol Indic 77: 386-396

Casatti L, Ferreira CP, Carvalho FR (2009) Grass-dominated stream sites exhibit low fish species diversity and dominance by guppies: an assessment of two tropical pasture River basins. Hydrobiologia 632: 273-283

Cassey P, Delean S, Lockwood JL, Sadowski JS, Blackburn TM (2018) Dissecting the null model for biological invasions: A meta-analysis of the propagule pressure effect. PLoS Biol 16(4): e2005987. https://doi.org/10.1371/journal. pbio.2005987

Cemig (2019a) Bacia do Rio Jequitinhonha. Peixe Vivo, Cemig – Companhia Energética de Minas Gerais. http://www.cemig.com.br/pt-br/A_Cemig_e_o_Futuro/sustentabilidade/nossos_programas/ambientais/peixe_vivo/Paginas/rio_jequitinhonha.aspx. Accessed 19 November 2019

Cemig (2019b) Bacias do Leste. Peixe Vivo, Cemig – Companhia Energética de Minas Gerais. http://www.cemig.com.br/pt-br/A_Cemig_e_o_Futuro/sustentabilidade/nossos_programas/ambientais/peixe_vivo/Paginas/bacias_do_leste.aspx. Accessed 19 November 2019

Cemig (2019c) Bacia do Rio Doce. Peixe Vivo, Cemig – Companhia Energética de Minas Gerais. http://www.cemig.com.br/pt-br/A_Cemig_e_o_Futuro/sustentabilidade/nossos_programas/ambientais/peixe_vivo/Paginas/rio_doce.aspx. Accessed 19 November 2019

Cemig (2019d) Bacia do Rio Paraíba do Sul. Peixe Vivo, Cemig – Companhia Energética de Minas Gerais. http://www.cemig.com.br/pt-br/A_Cemig_e_o_Futuro/sustentabilidade/nossos_programas/ambientais/peixe_vivo/Paginas/rio_paraiba.aspx. Accessed 19 November 2019

Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC (2017) Invasion Biology: Specific Problems and Possible Solutions. Trends Ecol Evol 32 (1): pp. 13-22. http://dx.doi.org/10.1016/j.tree.2016.11.001

Cucherousset J, Olden JD (2011) Ecological Impacts of Non-native Freshwater Fishes. Fisheries 36 (5)

Daga VS, Skóra F, Padial AA, Abilhoa V, Gubiani ÉA, Vitule JRS (2015) Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. Hydrobiologia 746: 327-47

Dawson W, Moser D, van Kleunen M, Kreft H, Pergl J, Pyšek P, Weigelt P, Winter M, Lenzner B, Blackburn TM, Dyer EED, Cassey P, Scrivens SL, Economo EP, Guénard B, Capinha C, Seebens H, García-Díaz P, Nentwig W, García-Berthou E, Casal C, Mandrak NE, Fuller P, Meyer C, Essl F (2017) Global hotspots and correlates of alien species richness across taxonomic groups. Nat Ecol Evol 1: 0186. doi:10.1038/s41559-017-0186

Duggan I, Rixon CAM, MacIsaac HJ (2006) Popularity and propagule pressure: determinants of introduction and establishement of aquarium fish. Biol Invas 8: 377- 382

Econservation (2019) Programa de Monitoramento da Ictiofauna do Rio Doce nos Estados de Minas Gerais e Espírito Santo – Atendimento a Cláusula 164 do Termo de Transação e de

Ajustamento de Conduta Alínea A, Ofício SEI nº 132/2016-DIBIO/ICMBIO – Relatório Final Relatório Técnico – RT ECV 260/18. 363 p.

FAO (2016). The state of world fisheries and aquaculture 2016. Rome, Italy: FAO. https://doi.org/10.18356/ 8e4e0 ebf-en

Fernandes GW, Goulart FF, Ranieri BD, Coelho MS, Dales K, Boesche N, Bustamante M, Carvalho FA, Carvalho DC, Dirzo R, Fernandes S, Galetti PM, Millan VEG, Mielke C, Ramirez JL, Neves A, Rogass C, Ribeiro SP, Scariot A, Soares-Filho B (2016) Deep into the mud: ecological and socio-economic impacts of the dam breach in Mariana, Brazil. Nat Conserv 14 (2): 35-45

Flecker AS (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77:1845–1854

Fragoso-Moura EN, Oporto LT, Maia-Barbosa P M, Barbosa FAR (2016) Loss of biodiversity in a conservation unit of the Brazilian Atlantic Forest: the effect of introducing non-native fish species. Braz J Biol, 76 (1): 18-27

Fricke R, Eschmeyer WN, Van der Laan R (2020) Eschmeyer's Catalog of Fishes: Genera, Species, references. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Accessed 26 April 2020

Froese R, Pauly D (2019). FishBase. World Wide Web electronic publication. www.fishbase.org

Garcia DAZ, Britton JR, Vidotto-Magnoni AP, Orsi ML (2018) Introductions of non-native fishes into a heavily modified river: rates, patterns and management issues in the Paranapanema River (Upper Paraná ecoregion, Brazil). Biol Invasions 20: 1229-1241

Garcia DA, Magalhães ALB, Vitule JRS, Casimiro ACR, Lima-Junior DP, Cunico AM, Britto MFG, Petrere-Junior M, Agostinho AA, Orsi ML (2018) The same old mistakes in aquaculture: the newly-available striped catfish *Pangasianodon hypophthalmus* is on its way to putting Brazilian freshwater ecosystems at risk. Biodivers Conserv 27 (13): 3545-3558

Giacomini HC, Lima Jr. DP, Latini AO, Espírito-Santo H.MV (2011) Spatio-temporal segregation and size distribution of fish assemblages as related to non-native species occurrence in the middle rio Doce Valley, MG, Brazil. Neotrop Ichthyol 9 (1): 135-146. doi:10.1590/s1679-62252011005000011

Godinho AL, Godinho HP (2003) Breve visão do São Francisco. In: Godinho HP, Godinho AL (ed) Águas, peixes e pescadores do São Francisco das Minas Gerais. PUC Minas, Belo Horizonte, pp 15-24

Gomes LC, Pessali TC, Sales NG, Pompeu PS, Carvalho DC (2015) Integrative taxonomy detects cryptic and overlooked fish species in a neotropical river basin. Genetica 143 (5). doi 10.1007/s10709-015-9856-z

Gubiani ÉA, Ruaro R, Ribeiro VR, Eichelberger ACA, Bogoni RF, Lira AD, Cavalli D, Piana PA, da Graça WJ (2018) Non-native fish species in Neotropical freshwaters: how did they arrive, and where did they come from? Hydrobiologia 817 (1): 57-69

Gurgel JJS, Oliveira AG (1987) Efeitos da introdução de peixes e crustáceos no semi-árido do nordeste brasileiro. Coleção Mossoroense, 453: 7-32

Ingenito LFS, Buckup PA (2007) The Serra da Mantiqueira, south-eastern Brazil, as a biogeographical barrier for fishes. J Biogeogr 34: 1173-1182. doi:10.1111/j.1365-2699.2007.01686.x

Instituto Brasileiro de Geografia e Estatística – IBGE (2020) https://www.ibge.gov.br. Accessed 25 February 2020

IUCN (2020) IUCN - EICAT Categories and Criteria: first edition. IUCN, Gland, Switzerland and Cambridge, UK

Jégu M (2003) Subfamily Serrasalminae (pacus and piranhas). In: Reis RE, Kullander SO, Ferraris Jr CJ (ed) Check list of Freshwater Fishes of South and Central America. Edipucrs, Porto Alegre, pp 182-196

Jeschke JM, Bacher S, Blackburn TM, Dick JT, Essl F, Evans T, Gaertner M, Hulme PE, Kühn I, Mrugała A, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Winter M, Kumschick S (2014) Defining the Impact of Non-Native Species. Conserv Biol 28: 1188-1194. doi:10.1111/cobi.12299

Ju R, Li X, Jiang J, Wu J, Liu J, Strong D R, Li B (2019). Emerging risks of non-native species escapes from aquaculture: Call for policy improvements in China and other developing countries. J Appl Ecol 00: 1-6. doi:10.1111/1365-2664.13521

Júlio-Júnior HF, Dei Tos C, Agostinho AA, Pavanelli CS (2009) A massive invasion of fish species after eliminating a natural barrier in the upper rio Paraná basin. Neotrop Ichthyol 7 (4):709-18

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan- European review. Aquatic Inva 9 (4): pp. 391- 423

Kohler HC (2003) Aspectos geoecológicos da bacia hidrográfica do São Francisco (primeira aproximação na escala 1:1 000 000). In: Godinho HP, Godinho AL (ed) Águas, peixes e pescadores do São Francisco das Minas Gerais. PUC Minas, Belo Horizonte, pp 25-35

Kovalenko KE, Dibble ED, Agostinho AA, Cantanhêde G, Fugi R (2010) Direct and indirect effects of an introduced piscivore, *Cichla kelberi* and their modification by aquatic plants. Hydrobiologia. 638: 245-253. https://doi.org/10.1007/s10750-009-0049-6

Kullander SO (2003) Family Cichlidae (Cichlids). In: Reis ER, Kullander SO, Ferraris-Jr CJ (ed) Check list of the freshwater fishes of South and Central America. Porto Alegre, EDIPUCRS, pp 605-654

Langeani F, Castro RMC, Oyakawa OT, Shibatta OA, Pavanelli CS, Casatti L (2007) Diversidade da ictiofauna do Alto Rio Paraná: composição atual e perspectivas futuras. Biota Neotrop 7 (3): 181-197

Latini AO (2001) Estado atual e perspectivas para a ictiofauna da região do Parque Estadual do Rio Doce, MG. In: Instituto Estadual de Florestas & Projeto Doces Matas (ed) Plano de Manejo do Parque Estadual do Rio Doce, MG. Belo Horizonte, pp 1-49

Latini AO (2016) Em destaque: *Pygocentrus nattereri* Kner, 1858. MG. Biota 9 (1): 39-40

Latini AO, Petrere-Jr. M (2004) Reduction of a native fish fauna by alien species: an example from Brazilian freshwater tropical lakes. Fisheries Manag Ecol 11: 71-79

Latombe G, Pyšek P, Jeschke JM, Blackburn TM, Bacher S, Capinha C, Costello MJ, Fernandez M, Gregory RD, Hobern D, Hui C, Jetz W, Kumschick S, McGrannachan C, Pergl J, Roy HE, Scalera R, Squires ZE, Wilson JRU, Winter M, Genovesi P, McGeoch MA (2016) A vision for global monitoring of biological invasions. Biol Conserv. http://dx.doi.org/10.1016/j.biocon.2016.06.013

Lima-Junior DP, Magalhães ALB, Pelicice FM, Vitule JRS, Azevedo-Santos VM, Orsi ML, Simberloff D, Agostinho AA (2018) Aquaculture expansion in Brazilian freshwaters against the Aichi Biodiversity Targets. Ambio 47: 427-440

Livengood EJ, Chapman FA (2011) The aquarium fish trade: an introduction with perspectives for responsible aquarium fish ownership. Univ. of Florida. FA124: 1-8. http://edis.ifas.ufl.edu/fa124

Lockwood JL, Cassey P, Blackburn TM (2009). The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Divers Distrib 15(5), 904-910. doi:10.1111/j.1472-4642.2009.00594.x

Magalhães ALB, Daga VS, Bezerra LAV, Vitule JRS, Jacobi CM, Silva LGM (2020) All the colors of the world: biotic homogenization-differentiation dynamics of freshwater fish communities on demand of the Brazilian aquarium trade. Hydrobiologia. https://doi.org/10.1007/s10750-020-04307-w

Magalhães ALB, Jacobi CM (2013a) Asian aquarium fishes in a Neotropical biodiversity hotspot: impeding establishment, spread and impacts. Biol Invas 15 (10), 2157–2163

Magalhães ALB, Jacobi CM (2013b) Invasion risks posed by ornamental freshwater fish trade to southeastern Brazilian rivers. Neotrop Ichthyol 11 (2): 433-441

Magalhães ALB, Jacobi CM (2017) Colorful invasion in permissive Neotropical ecosystems: Establishment of ornamental non-native poeciliids of the genera *Poecilia/Xiphophorus* (Cyprinodontiformes: Poeciliidae) and management alternatives. Neotrop Ichthyol 15: e160094

Magalhães ALB, Orsi ML, Pelicice FM, Azevedo-Santos VM, Vitule JRS, Lima-Junior DP, Brito MFG (2017) Small size today, aquarium dumping tomorrow: sales of juvenile non-native large fish as an important threat in Brazil. Neotrop Ichthyol 15: e170033

Magalhães ALB, Brito MFG, Sarrouh B (2019) An inconvenient routine: introduction, establishment and spread of new non-native fishes in the Paraíba do Sul River basin, state of Minas Gerais, Brazil. Neotrop Biol Conserv 14 (3): 329-338

Makrakis S, Gomes LC, Makrakis MC, Fernandez DR, Pavanelli CS (2007) The Canal da Piracema at Itaipu Dam as a fish pass system. Neotrop Ichthyol 5 (2): 185-95

Mandrak NE, Cudmore B (2010) The fall of Native Fishes and the rise of Non-native Fishes in the Great Lakes Basin. Aquatic Ecosyst Health Manag 13 (3): 255-268

Martins ML (2008) O Jequitinhonha dos viajantes, séculos XIX e XX: olhares diversos sobre as relações sociedade – natureza no nordeste mineiro. Varia Historia 24 (40): 707-728

Melo CE, Röpke CP (2004) Alimentação e distribuição de piaus (Pisces, Anostomidae) na Planície do Bananal, Mato Grosso, Brasil. Rev Bras Zool 21 (1). https://doi.org/10.1590/S0101-81752004000100010

Mendoza R, Koleff P (2014) Introducción de especies exóticas acuáticas en México y en el mundo. In: Mendoza R, Koleff P (ed). Especies acuáticas invasoras en México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, pp 17-41

Ng C (2016) The ornamental freshwater fish trade in Malaysia. UTAR Agric Sci J 2: 7-18

Ng PK, Tan H (1997) Freshwater fishes of Southeast Asia: potential for the aquarium fish trade and conservation issues. Aquar Sci Conserv 1: 79–90. https://doi.org/10.1023/A:1018335617835

N'Guyen A, Hirsch PE, Bozzuto C, Adrian-Kalchhauser I, Hôrková K, Burkhardt-Holm P (2018) A dynamical model for invasive round goby populations reveals efficient and effective management options. J Appl Ecol 55: 342-352. https://doi.org/10.1111/1365-2664.12934

Nobile AB, Cunico AM, Vitule JRS, Queiroz J, Vidotto-Magnoni AP, Garcia DAZ, Orsi ML, Lima FP, Acosta AA, Silva RJ, Prado FD, Porto-Foresti F, Brandão H, Foresti F, Oliveira C, Ramos IP (2019) Status and recommendations for sustainable freshwater aquaculture in Brazil. Rev Aquaculture. https://doi.org/10.1111/raq.12393

Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. J Biogeogr 33: 2027-2039

Oyakawa OT, Menezes NA (2011) Checklist dos peixes de água doce do Estado de São Paulo, Brasil. Biota Neotropica 11 (suppl 1): 19-32. doi:10.1590/s1676060320110005000002

Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as a source of invasive species in aquatic ecosystems. Front Ecol Environ 2: 131-38

Patoka J, Magalhães ALB, Kouba A, Faulkes Z, Jerikho R, Vitule JRS (2018) Invasive aquatic pets: failed policies increase risks of harmful invasions. Biodivers Conserv 27: 3037-3046

Pelicice FM, Agostinho AA (2009) Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biol Invasions. 11: 1789-1801

Pelicice FM, Azevedo-Santos VM, Vitule JRS, Orsi ML, Lima-Junior DP, Magalhães ALB, Pompeu PS, Petrere-Junior M, Agostinho AA (2017) Neotropical freshwater fishes imperilled by unsustainable policies. Fish and Fisheries 18 (6): 1119-1133

Pelicice FM, Vitule JRS, Lima-Junior DP, Orsi ML, Agostinho AA (2014) A serious new threat to Brazilian freshwater ecosystems: The naturalization of nonnative fish by decree. Conserv Lett 7(1): 55-60

Pelicice FM, Latini JD, Agostinho AA (2015) Fish fauna disassembly after the introduction of a voracious predator: main drivers and the role of the invader's demography. Hydrobiologia 746: 271-283

Pinto-Coelho RM, Bezerra-Neto JF, Miranda F, Mota TG, Resck R, Santos AM et al. (2008) The inverted trophic cascade in tropical plankton communities: impacts of exotic fish in the Middle Rio Doce lake district, Minas Gerais, Brazil. Braz J Biol 68 (4 Suppl): 1025-1037

Pompeu PS (2010) Os peixes do rio Mucuri. MG. Biota 2 (5): 36-43

Pugedo ML, Andrade FR, Pessali TC, Birindelli JLO, Carvalho DC (2016) Integrative taxonomy supports new candidate fish species in a poorly studied neotropical region: The Jequitinhonha River Basin. Genetica. doi 10.1007/s10709-016-9903-4

Pyšek P, Meyerson LA, Simberloff D (2018) Introducing "Alien Floras and Faunas", a new series in Biological Invasions. Biol Invas. https://doi.org/10.1007/s10530-017-1648-1

Pyšek P, Dawson W, Essl F, Kreft H, Pergl J, Seebens H, van Kleunen M, Weigelt P, Winter M (2019) Contrasting patterns of naturalized plant richness in the Americas: Numbers are higher in the North but expected to rise sharply in the South. Global Ecol Biogeogr 1-5. doi: 10.1111/geb.12891

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/

Reis RE, Albert JS, Di Dario F, Mincarone MM, Petry P, Rocha LA (2016) Fish biodiversity and conservation in South America. J Fish Biol 89: 12-47. doi:10.1111/jfb.13016

Reis VJC (2018) Diversity of the genus *Trichomycterus* Valenciennes, 1832 (Siluriformes, Trichomycteridae) in the Rio Doce basin: A systematic study integrating phenotypes, DNA and classical taxonomy (Unpublished Master thesis). University of São Paulo, São Paulo, Brazil. 303 p.

Ribeiro DC, Chagas JMA, Thereza MR, Langeani F (2019) Checklist and key for the identification of fish fauna of the Uberaba River, Upper Paraná River system, Brazil. ZooKeys 875: 129-155. doi: 10.3897/zookeys.875.31977

Ricciardi A, Blackburn TM, Carlton JT, Dick JTA, Hulme PE, Iacarella JC, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, Pyšek P, Richardson DM, Ruiz GM, Simberloff D, Sutherland WJ, Wardle DA, Aldridge DC (2017). Invasion Science: A Horizon Scan of Emerging Challenges and Opportunities. 32 (6): pp 464-474. http://dx.doi.org/10.1016/j.tree.2017.03.007

Ribeiro LB, Matoso DA, Feldberg E (2014) Chromosome mapping of repetitive sequences in four Serrasalmidae species (Characiformes). Genet Mol Biol 37 (1): 46-53

Sales NG, Pessali TC, Andrade FR, Carvalho DC (2018) Introgression from non-native species unveils a hidden threat to the migratory Neotropical fish *Prochilodus hartii*. Biol Invas. 20: 555-566

Salvador GN, Frederico RG, Pessali TC, Vieira F, Freitas TMS (2018) Length-weight relationship of 21 fish species from Rio Doce River basin, Minas Gerais, Brazil. J Appl Ichthyol 00:1-4. https://doi.org/10.1111/jai.13734

Silva PA, Vieira GG, Farinasso M, Carlos RJ (2003) Determinação da extensão do rio São Francisco. Anais XI SBSR, Belo Horizonte, 393-400

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40: 81-102

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García- Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28 (1): 58-66

Taylor BW, Flecker AS, Hall-Jr RO (2006) Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science 313 (5788): 833-836. https://doi.org/10.1126/science.1128223

Teixeira DF, Neto FRA, Gomes LC, et al. (2020) Invasion dynamics of the white piranha (*Serrasalmus brandtii*) in a Neotropical river basin. Biol Invasions 22: 983-995. https://doi.org/10.1007/s10530-019-02138-y

Teixeira TP, Pinto BCT, Terra BF, Estiliano EO, Gracia D, Araújo FG (2005) Diversidade das assembleias de peixes nas quatro unidades geográficas do rio Paraíba do Sul. Iheringia 95(4): 347-357

Teletchea F (2016) Domestication level of the most popular aquarium fish species: is the aquarium trade dependent on wild populations? Cybium 40 (1): 21-29

Vieira F, Rodrigues RR (2010) A fauna de peixes dos afluentes do rio Paraíba do Sul no estado de Minas Gerais. MG. Biota 3 (1): 5-23

Vieira F (2010) Distribuição, impactos ambientais e conservação da fauna de peixes da bacia do rio Doce. MG. Biota 2 (5): 5-22

Vinogradova Y, Pergl J, Essl F, Hejda M, van Kleunen M, Regional contributors, Pyšek P (2018) Invasive alien plants of Russia: insights from regional inventories. Biol Invas. https://doi.org/10.1007/s10530-018-1686-3

Vitule JRS, Freire CA, Simberloff D (2009) Introduction of non-native freshwater fish can certainly be bad. Fish and Fisheries 10: 98-108

Vitule JRS, Occhi TVT, Kang B, Matsuzaki SI, Bezerra LA, Daga VS, Faria L, Frehse FA, Walter F, Padial AA (2019) Intra-country introductions unraveling global hotspots of alien fish species. Biodivers Conserv 28 (11): 3037-3043. https://doi.org/10.1007/s10531-019-01815-7

Vitule JRS, Skora F, Abilhoa V (2012) Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. Divers Distrib 18: 111-120

Welcomme RL (1988) International introductions of inland aquatic species. FAO Fish Tech Pap. 294: 1-318

Winemiller KO, Jepsen DB (1998) Effects of seasonality and fish movement on tropical river food webs. J Fish Biol 53: 267-296. https://doi.org/10.1111/j.1095-8649.1998.tb01032.x

Zenni RD (2014) Analysis of introduction history of invasive plants in Brazil reveals patterns of association between biogeographical origin and reason for introduction. Aust Ecol 39: 401-407

SUPPLEMENTARY MATERIAL

Table 1 List of freshwater alien fish species introduced in southeastern Brazil watersheds (Upper Paraná, Doce, Jequitinhonha, Mucuri, Paraíba do Sul, and São Francisco), with information on species invasion status accordinng Blackburn et al. 2011 (C = casual, D = naturalized, E = invasive, N = native, A = absent), environmental impact category according to Blackburn et al. 2014 and EICAT (MV = massive, MR = major, MO = moderate, DD = data deficient, DD* = data deficient, but the species probably impacts the recipient environment), pathways of introduction, origin and species taxonomic attributes.

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
ANABANTIFORMES										
Helostomatidae										
Helostoma temminckii Cuvier 1829	A	A	A	A	C	A	DD	aquarium trade	Asia	Magalhães 2007; Latini et al. 2016
Osphronemidae										
Betta splendens Regan 1910	A	A	A	A	C	C	DD	aquarium trade	Asia	Magalhães and Jacobi 2008; Latini et al. 2016; Magalhães et al. 2016
Macropodus opercularis (Linnaeus 1758)	A	A	A	A	D	A	DD	aquarium trade	Asia	Alves et al. 2007; Magalhães and Jacobi 2013; Moraes et al. 2017
Trichogaster chuna (Hamilton 1822)	A	A	A	A	C	A	DD	aquarium trade	Asia	Alves et al. 2007, Moraes et al. 2017
Trichogaster lalius (Hamilton 1822)	A	A	A	A	C	A	DD	aquarium trade	Asia	Alves et al. 2007, Moraes et al. 2017
Trichopodus pectoralis Regan 1910	A	A	A	A	C	A	DD	aquarium trade	Asia	Latini et al. 2016, Moraes et al. 2017
Trichopodus trichopterus (Pallas 1770)	A	A	A	A	C	C	DD	aquarium trade	Asia	Alves et al. 2007, Moraes et al. 2017
ATHERINIFORMES										
Atherinopsidae										
Odontesthes bonariensis (Valenciennes 1835)	C	A	A	A	A	A	DD*	geographical barrier	South America	Alves et al. 2007; Langeani et al. 2007; Santos 2010

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
CENTRARCHIFORMES										
Centrarchidae										
Lepomis gibbosus (Linnaeus 1758)	A	D	A	A	A	A	DD	fishing	North America	Magalhães and Ratton 2005; Alves et al. 2007; Vieira 2010
Micropterus salmoides (Lacepède 1802)	C	D	A	A	D	A	DD	fishing	North America	Bizerril and Primo 2001; Alves et al. 2007; Langeani et al. 2007, Santos 2010; Rocha et al. 2011
CERATODONTIFORMES										
Lepidosirenidae										
Lepidosiren paradoxa Fitzinger 1837	A	A	A	A	A	C	DD	unknown	South America	Alves et al. 2007
CICHLIFORMES										
Cichlidae										
Aequidens plagiozonatus Kullander 1984	C	A	A	A	A	A	DD	aquarium trade	South America	Ota et al. 2018
Aequidens sp.	A	A	A	A	C	A	DD	aquarium trade	South America	Bizerril and Primo 2001; Teixeira et al. 2005
Apistogramma commbrae (Regan 1906)	C	A	A	A	A	A	DD	aquarium trade and geographical barrier	South America	Ota et al. 2018
Astronotus crassipinnis (Heckel 1840)	D	D	A	A	A	A	DD*	aquarium trade and biological control	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Langeani and Rêgo 2014; Sanches et al. 2014; Ota et al. 2018
Astronotus ocellatus (Agassiz 1831)	A	D	C	A	C	D	DD*	aquarium trade and biological control	South America	Alves et al. 2007; Andrade-Neto 2010; Vieira 2010; Rocha et al. 2011; Barbosa et al. 2017; Magalhães et al. 2019
Chaetobranchopsis australis Eigenmann & Ward 1907	C	A	A	A	A	A	DD	aquarium trade	South America	Ota et al. 2018
Cichla kelberi Kullander & Ferreira 2006	E	E	A	A	D	E	MV	fishing	South America	Alves et al. 2007; Santos 2010; Sanches et al. 2014; Moraes et al. 2017; Ota et al. 2018
Cichla monoculus Spix & Agassiz 1831	A	A	A	A	A	D	DD*	fishing	South America	Pompeu and Alves 2003; Pers. Com. Pessali TC
Cichla ocellaris Bloch & Schneider 1801	A	A	A	A	D	D	DD*	fishing	South America	Moraes et al. 2017; Bartolette et al. 2018; Pers. Com. Pessali TC

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Cichlidae										
Cichla piquiti Kullander & Ferreira 2006	E	A	A	E	E	E	DD*	fishing	South America	Langeani et al. 2007; Santos 2010; Langeani and Rêgo 2014; Sanches et al. 2014; Barbosa et al. 2017; Ota et al. 2018
Cichla temensis Humboldt 1821	A	A	A	A	C	A	DD	fishing	South America	Bizerril and Primo 2001
Cichla sp.	A	A	D	A	A	A	DD	fishing	South America	Pers. Com. Pessali TC
Cichlasoma dimerus (Heckel 1840)	A	A	A	A	E	A	DD	aquarium trade	South America	Bartolette et al. 2019
Cichlasoma portalegrense (Hensel 1870)	A	A	A	A	C	A	DD	aquarium trade	South America	Honorio and Martins 2018
Coptodon rendalli (Boulenger 1897)	E	E	E	E	E	E	DD*	aquaculture	Africa	Alves et al. 2007; Langeani et al. 2007; Andrade-Neto 2010; Santos 2010; Vieira 2010; Rocha et al. 2011; Langeani and Rêgo 2014; Sanches et al. 2014; Barbosa et al. 2017; Moraes et al. 2017; Ota et al. 2018; Bartolette et al. 2018
Crenicichla macrophthalma Heckel 1840	A	A	A	A	C	A	DD	aquaculture	South America	Latini et al. 2016
Crenicichla semifasciata (Heckel 1840)	C	A	A	A	A	A	DD	unknown	South America	Roa-Fuentes et al. 2015
Geophagus sveni Lucinda, Lucena & Assis 2010	E	A	A	A	A	A	DD*	aquarium trade	South America	Langeani et al. 2007; Sanches et al. 2014; Ota et al. 2018
Hemichromis bimaculatus Gill 1862	A	A	A	A	C	A	DD	aquarium trade	Africa	Alves et al. 2007; Moraes et al. 2017
Heterotilapia buttikoferi (Hubrecht 1881)	C	A	A	A	A	A	DD*	aquarium trade	Africa	Sampaio et al. 2017
Laetacara araguaiae Ottoni & Costa 2009	C	A	A	A	A	A	DD	aquarium trade	South America	Ota et al. 2018
Laetacara curviceps (Ahl 1923)	A	A	A	A	D	A	DD	aquarium trade	South America	Alves et al. 2007; Moraes et al. 2017
Mikrogeophagus altispinosus (Haseman 1911)	A	A	A	A	D	A	DD	aquarium trade	South America	Magalhães 2007; Latini et al. 2016
Mikrogeophagus ramirezi (Myers & Harry 1948)	A	A	A	A	D	A	DD	aquarium trade	South America	Alves et al. 2007; Moraes et al. 2017

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Cichlidae										
Oreochromis niloticus (Linnaeus 1758)	E	E	E	E	E	E	DD*	aquaculture	Africa	Teixeira et al. 2005; Alves et al. 2007; Langeani et al. 2007; Andrade-Neto 2010; Pompeu 2010; Santos 2010; Vieira 2010; Rocha et al. 2011; Langeani and Rêgo 2014; Sanches et al. 2014; Barbosa et al. 2017; Moraes et al. 2017; Honorio and Martins 2018; Ota et al. 2018; Bartolette et al. 2018
Parachromis managuensis (Günther 1867)	A	D	A	A	C	D	DD	aquarium trade	Central America	Barros et al. 2012; Barbosa et al. 2017; Moraes et al. 2017
Pelvicachromis pulcher (Boulenger 1901)	A	A	A	A	C	A	DD	aquarium trade	Africa	Magalhães 2007; Latini et al. 2016; Moraes et al. 2017
Pterophyllum scalare (Schultze 1823)	A	A	A	A	D	A	DD	aquarium trade	South America	Alves et al. 2007; Moraes et al. 2017
Satanoperca pappaterra (Heckel 1840)	E	A	A	A	C	A	DD	aquaculture	South America	Alves et al. 2007; Langeani et al. 2007; Santos 2010; Langeani and Rêgo 2014; Sanches et al. 2014; Bartolette et al. 2018
CHARACIFORMES										
Acestrorhynchidae										
Acestrorhynchus pantaneiro Menezes 1992	C	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Anostomidae										
Abramites hypselonotus (Günther 1868)	A	A	A	A	C	A	DD	aquarium trade	South America	Teixeira et al. 2005
Leporinus geminis Garavello & Santos 2009	C	A	A	A	A	A	DD	unknown	South America	Langeani and Rêgo 2014; Sanches et al. 2014
Leporinus octofasciatus Steindachner 1915	N	A	A	A	A	C	DD	aquarium trade	South America	Moreira-Filho et al. 2006
Leporinus taeniatus Lütken 1875	A	A	D	A	A	N	DD	unknown	South America	Andrade-Neto 2010, Pugedo et al. 2016
Leporinus tigrinus Borodin 1929	D	A	A	A	A	A	DD	unknown	South America	Ota et al. 2018
Megaleporinus macrocephalus (Garavello & Britski 1988)	E	D	C	C	C	C	DD	aquaculture	South America	Alves et al. 2007; Langeani et al. 2007; Pompeu 2010; Santos 2010; Vieira 2010; Langeani and Rêgo 2014; Sanches et al. 2014; Moraes et al. 2017; Ota et al. 2018; Pers. Com. Pessali TC

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Anostomidae										
Megaleporinus obtusidens (Valenciennes 1837)	N	D	A	A	A	N	DD	aquaculture	South America	Pers. Com. Pessali TC
Schizodon borellii (Boulenger 1900)	E	A	A	A	A	A	DD	aquaculture	South America	Ota et al. 2018
Synaptolaemus latofasciatus (Steindachner 1910)	A	A	A	A	C	A	DD	aquarium trade	South America	Bartolette et al. 2019
Bryconidae										
Brycon amazonicus (Agassiz 1829)	C	C	A	A	C	C	DD*	aquaculture	South America	Oyakawa and Menezes 2011; Barbosa et al. 2017 ; Moraes et al. 2017
Brycon hilarii (Valenciennes 1850)	C	A	A	A	A	C	DD*	aquaculture	South America	Langeani et al. 2007; Barbosa et al. 2017; Ota et al. 2018
Brycon orbignyanus (Valenciennes 1850)	N	A	A	A	C	A	DD	aquaculture	South America	Moraes et al. 2017
Brycon vonoi Lima 2017	A	A	C	A	A	A	DD	aquaculture	South America	Pers. Com. Pessali TC
Salminus brasiliensis (Cuvier 1816)	N	E	A	C	E	A	DD*	fishing and aquaculture	South America	Teixeira et al. 2005; Alves et al. 2007; Vieira 2010; Moraes et al. 2017
Characidae										
Aphyocharax anisitsi Eigenmann & Kennedy 1903	N	A	A	A	C	A	DD	aquarium trade	South America	Magalhães et al. 2019
Aphyocharax dentatus Eigenmann & Kennedy 1903	C	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Bryconamericus exodon Eigenmann 1907	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007, Ota et al. 2018
Bryconamericus iheringii (Boulenger 1887)	A	A	A	A	C	A	DD	unknown	South America	Honorio and Martins 2018
Cynopotamus kincaidi (Schultz 1950)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007
Gymnocorymbus ternetzi (Boulenger 1895)	C	A	A	A	D	A	DD	aquarium trade	South America	Alves et al. 2007; Langeani et al. 2007; Santos 2010; Moraes et al. 2017
Hemigrammus ora Zarske, Le Bail & Géry 2006	C	A	A	A	A	A	DD	unknown	South America	Ota et al. 2018
Hyphessobrycon eques (Steindachner 1882)	E	E	A	A	E	D	DD	aquarium trade	South America	Alves et al. 2007; Santos 2010; Vieira 2010; Moraes et al. 2017; Honorio and Martins 2018; Ota et al 2018 ; Bartolette et al. 2018

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Characidae										
Hyphessobrycon flammeus Myers 1924	C	A	A	A	N	A	DD	aquarium trade	South America	Langeani et al. 2007
Hyphessobrycon herbertaxelrodi Géry 1961	A	A	A	A	D	A	DD	aquarium trade	South America	Magalhães and Carvalho 2007
Hyphessobrycon moniliger Moreira, Lima & Costa 2002	C	A	A	A	A	A	DD	aquarium trade	South America	Ota et al. 2018
Hyphessobrycon reticulatus Ellis 1911	C	A	A	A	A	A	DD	unknown	South America	Santos and Esteves 2014
Knodus moenkhausii (Eigenmann & Kennedy 1903)	E	E	E	E	E	E	DD	aquarium trade	South America	Langeani et al. 2007; Langeani and Rêgo 2014; Ota et al. 2018; Salvador et al. 2018 ; Magalhães et al. 2019
Mimagoniates microlepis (Steindachner 1877)	A	A	A	A	C	A	DD	aquarium trade	South America	Pers. Com. Magalhães ALB
Moenkhausia australis Eigenmann 1908	D	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Moenkhausia costae (Steindachner 1907)	D	A	E	A	C	N	DD	aquarium trade	South America	Andrade-Neto 2010; Langeani and Rêgo 2014; Sanches et al. 2014; Magalhães et al. 2019
Moenkhausia forestii Benine, Mariguela & Oliveira 2009	C	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Odontostilbe microcephala Eigenmann 1907	C	A	A	A	A	A	DD	unknown	South America	Carmassi et al. 2012
Psellogrammus kennedyi (Eigenmann 1903)	C	A	A	A	A	N	DD	geographical barrier	South America	Ota et al. 2018
Pseudocorynopoma heterandria Eigenmann 1914	A	A	A	A	C	A	DD	unknown	South America	Salgado et al. 2015; Moraes et al. 2017
Roeboides descalvadensis Fowler 1932	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Sanches et al. 2014, Ota et al. 2018
Serrapinnus calliurus (Boulenger 1900)	C	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Crenuchidae										
Characidium lagosantense Travassos 1947	C	A	A	A	A	N	DD	unknown	South America	Ribeiro et al. 2016
Characidium laterale (Boulenger 1895)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007
Characidium pterostictum Gomes 1947	A	A	A	A	C	A	DD	unknown	South America	Honorio and Martins 2018
Curimatidae										
Cyphocharax gillii (Eigenmann & Kennedy 1903)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007
Steindachnerina brevipinna (Eigenmann & Eigenmann 1889)	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Erythrinidae										
Erythrinus erythrinus (Bloch & Schneider 1801)	E	A	A	A	A	A	DD	geographical barrier and live bait	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Hoplerythrinus unitaeniatus (Spix & Agassiz 1829)	E	A	A	A	A	N	DD	geographical barrier and live bait	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Hoplias mbigua Azpelicueta, Benítez, Aichino & Mendez 2015	C	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Hemiodontidae										
Hemiodus orthonops Eigenmann & Kennedy 1903	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Ota et al. 2018
Lebiasinidae										
Nannostomus beckfordi Günther 1872	A	A	A	A	E	A	DD	aquarium trade	South America	Magalhães and Jacobi 2008; Latini et al. 2016; Magalhães et al. 2019
Pyrrhulina brevis Steindachner 1876	A	A	A	A	D	A	DD	aquarium trade	South America	Magalhães and Carvalho 2007; Latini et al. 2016

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Parodontidae										
Apareiodon affinis (Steindachner 1879)	N	A	A	A	D	A	DD	aquarium trade	South America	Honorio and Martins 2018
Apareiodon itapicuruensis Eigenmann & Henn 1916	A	A	A	A	C	A	DD	live bait	South America	Salgado et al. 2017
Apareiodon piracicabae (Eigenmann 1907)	N	A	A	A	D	N	DD	live bait	South America	Salgado et al. 2017; Bartolette et al. 2018
Prochilodontidae										
Prochilodus argenteus Spix & Agassiz 1829	A	C	E	C	A	N	MO	aquaculture	South America	Alves et al. 2007
Prochilodus costatus Valenciennes 1850	A	E	E	D	C	N	MO	aquaculture	South America	Alves et al. 2007; Andrade-Neto 2010; Pompeu 2010; Vieira 2010; Salvador et al. 2018
Prochilodus lineatus (Valenciennes 1837)	N	A	D	A	N	C	DD*	aquaculture	South America	Alves et al. 2007; Pers. Com. Pessali TC
Prochilodus nigricans Spix & Agassiz 1829	A	A	A	A	A	C	DD	aquaculture	South America	Pers. Com. Pessali TC
Prochilodus sp. "hybrid"	A	C	A	A	A	A	DD	unknown	South America	Pers. Com. Pessali TC
Serrasalmidae										
Colossoma macropomum (Cuvier 1816)	C	C	C	C	C	C	DD	fishing and aquaculture	South America	Alves et al. 2007; Langeani et al. 2007; Santos 2010; Vieira 2010; Rocha et al. 2011; Barbosa et al. 2017; Moraes et al. 2017; Ota et al. 2018; Pers. Com. Pessali TC
Metynnis lippincottianus (Cope 1870)	E	E	A	A	D	E	DD	aquarium trade	South America	Sanches et al. 2014; Moraes et al. 2017; Ota et al. 2018; Bartolette et al. 2018; Pers.Com. Pessali TC
Metynnis mola Eigenmann & Kennedy 1903	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007
Piaractus brachypomus (Cuvier 1818)	A	A	A	A	C	C	DD	fishing and aquaculture	South America	Latini et al. 2016; Moraes et al. 2017
Piaractus mesopotamicus (Holmberg 1887)	N	C	A	A	C	E	DD	fishing and aquaculture	South America	Alves et al. 2007; Vieira 2010; Barbosa et al. 2017; Latini et al. 2016; Moraes et al. 2017
Pygocentrus nattereri Kner 1858	C	E	A	A	A	A	MV	biological control and fishing	South America	Alves et al 2007; Vieira 2010; Langeani and Rêgo 2014; Sanches et al. 2014
Serrasalmus brandtii Lütken 1875	A	A	E	A	A	N	MO	unknown	South America	Andrade-Neto 2010

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Serrasalmidae										
Serrasalmus marginatus Valenciennes 1837	E	A	A	A	A	A	MO	geographical barrier	South America	Júlio-Júnior et al 2009; Langeani and Rêgo 2014; Ota et al. 2018
Colossoma macropomum x *Piaractus mesopotamicus* "hybrid"	A	C	A	A	C	A	DD	aquaculture	South America	Alves et al. 2007; Moraes et al. 2017; Bartolette et al. 2018
Triportheidae										
Triportheus nematurus (Kner 1858)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Langeani and Rêgo 2014; Sanches et al. 2014; Ota et al. 2018
Triportheus signatus (Garman 1890)	C	A	A	A	A	A	DD	live bait	South America	Rocha et al. 2011
CLUPEIFORMES										
Clupeidae										
Platanichthys platana (Regan 1917)	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Ota et al. 2018
CYPRINIFORMES										
Cobitidae										
Misgurnus anguillicaudatus (Cantor 1842)	A	A	A	A	E	A	MR	aquarium trade	Asia	Alves et al. 2007; Magalhães and Jacobi 2013; Moraes et al. 2017
Cyprinidae										
Barbodes semifasciolatus (Günther 1868)	A	A	A	A	C	A	DD	aquarium trade	Asia	Alves et al. 2007; Moraes et al. 2017
Carassius auratus (Linnaeus 1758)	A	A	A	A	D	A	MR	aquarium trade	Asia	Alves et al. 2007; Magalhães & Jacobi 2013; Moraes et al. 2017
Cyprinus carpio Linnaeus 1758	E	E	D	C	E	C	DD*	aquaculture	Asia and Europe	Alves et al. 2007; Langeani et al. 2007; Pompeu 2010; Santos 2010; Vieira 2010; Rocha et al. 2011; Barbosa et al. 2017; Moraes et al. 2017; Ota et al. 2018
Dawkinsia tambraparniei (Silas 1954)	A	A	A	A	D	A	DD	aquarium trade	Asia	Magalhães and Jacobi 2008; Magalhães and Jacobi 2013; Latini et al. 2016; Moraes et al. 2017
Oliotius oligolepis (Bleeker 1853)	A	A	A	A	C	A	DD	aquarium trade	Asia	Magalhães and Jacobi 2008; Latini et al. 2016; Moraes et al. 2017
Pethia conchonius (Hamilton 1822)	A	A	A	A	E	A	MR	aquarium trade	Asia	Alves et al. 2007; Magalhães and Jacobi 2013; Moraes et al. 2017

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Cyprinidae										
Pethia nigrofasciata (Günther 1868)	A	A	A	A	D	A	DD	aquarium trade	Asia	Alves et al. 2007; Magalhães and Jacobi 2013; Moraes et al. 2017
Pethia ticto (Hamilton 1822)	A	A	A	A	C	A	DD	aquarium trade	Asia	Magalhães and Jacobi 2008; Latini et al. 2016; Moraes et al. 2017
Puntigrus tetrazona (Bleeker 1855)	A	A	A	A	D	A	DD	aquarium trade	Asia	Alves et al. 2007; Moraes et al. 2017
Puntius sachsii (Ahl 1923)	A	A	A	A	C	A	DD	aquarium trade	Asia	Magalhães and Carvalho 2007; Latini et al. 2016
Puntius titteya Deraniyagala 1929	A	A	A	A	C	A	DD	aquarium trade	Asia	Magalhães and Jacobi 2008; Latini et al. 2016; Moraes et al. 2017
Danionidae										
Danio rerio (Hamilton 1822)	A	A	A	A	E	A	MR	aquarium trade	Asia	Alves et al. 2007; Magalhães and Jacobi 2013; Moraes et al. 2017
Danio rerio "transgenic" (GloFish®)	A	A	A	A	D	A	DD*	aquarium trade	Asia	Pers. Com. Magalhães ALB
Devario malabaricus (Jerdon 1849)	A	A	A	A	D	A	DD	aquarium trade	Asia	Alves et al. 2007; Magalhães and Jacobi 2013; Moraes et al. 2017
Tanichthyidae										
Tanichthys albonubes Lin 1932	A	A	A	A	C	A	DD	aquarium trade	Asia	Alves et al. 2007; Moraes et al. 2017
Xenocyprididae										
Ctenopharyngodon idella (Valenciennes 1844)	C	C	A	A	A	C	DD	aquaculture	Asia	Alves et al. 2007; Langeani et. al 2007; Vieira 2010; Santos 2010; Barbosa et al. 2017; Moraes et al. 2017
Hypophthalmichthys molitrix (Valenciennes 1844)	A	C	C	A	A	A	DD	unknown	Asia	Alves et al. 2007; Andrade-Neto 2010; Vieira 2010
Hypophthalmichthys nobilis (Richardson 1845)	C	C	A	A	C	A	DD	aquaculture	Asia	Alves et al. 2007; Langeani et al. 2007; Santos 2010; Vieira 2010; Moraes et al. 2017

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
CYPRINODONTIFORMES										
Poeciliidae										
Poecilia latipinna (Lesueur 1821)	A	A	A	A	C	C	DD	aquarium trade	North America	Magalhães and Jacobi 2008; Barbosa et al. 2017
Poecilia reticulata Peters 1859	E	E	E	E	E	E	DD*	aquarium trade and biological control	South America	Teixeira et al. 2005; Alves et al. 2007; Langeani et al. 2007; Andrade-Neto 2010; Pompeu 2010; Santos 2010; Vieira 2010; Langeani and Rêgo 2014; Barbosa et al. 2017; Magalhães and Jacobi 2017; Moraes et al. 2017; Ota et al. 2018
Poecilia sphenops Valenciennes 1846	A	A	A	A	E	D	MR	aquarium trade	Central America and South America	Alves et al. 2007; Magalhães and Jacobi 2017; Moraes et al. 2017
Poecilia velifera (Regan 1914)	A	A	A	A	D	A	DD	aquarium trade	Central America	Magalhães and Jacobi 2008; Latini et al. 2016; Magalhães and Jacobi 2017; Moraes et al. 2017
Poecilia vivipara Bloch & Schneider 1801	C	N	A	N	N	C	DD	aquarium trade and biological control	South America	Santos 2010; Barbosa et al. 2017
Xiphophorus hellerii Heckel 1848	D	C	A	A	E	C	DD	aquarium trade	Central America and North America	Alves et al. 2007; Langeani et al. 2007; Vieira 2010; Magalhães and Jacobi 2017; Moraes et al. 2017
Xiphophorus maculatus (Günther 1866)	C	A	A	A	E	A	DD	aquarium trade	Central America and North America	Alves et al. 2007; Langeani et al. 2007; Magalhães and Jacobi 2017; Moraes et al. 2017
Xiphophorus variatus (Meek 1904)	A	A	A	A	E	D	DD	aquarium trade	North America	Alves et al. 2007; Barbosa et al. 2017; Magalhães and Jacobi 2017; Moraes et al. 2017
Rivulidae										
Atlantirivulus santensis (Köhler 1906)	C	A	A	A	A	A	DD	unknown	South America	Santos and Esteves 2014

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
GYMNOTIFORMES										
Apteronotidae										
Apteronotus albifrons (Linnaeus 1766)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Ota et al. 2018
Apteronotus brasiliensis (Reinhardt 1852)	C	C	A	A	A	N	DD	live bait	South America	Langeani et al. 2007; Langeani and Rêgo 2014
Apteronotus caudimaculosus de Santana 2003	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Langeani and Rêgo 2014; Ota et al. 2018
Gymnotidae										
Gymnotus pantanal Fernandes, Albert, Daniel-Silva, Lopes, Crampton & Almeida-Toledo 2005	D	A	A	A	A	A	DD*	geographical barrier and live bait	South America	Júlio-Júnior et al. 2009; Ota et al 2018
Gymnotus paraguensis Albert & Crampton 2003	C	A	A	A	A	A	DD	geographical barrier and live bait	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al 2018
Hypopomidae										
Brachyhypopomus gauderio Giora & Malabarba 2009	E	A	A	A	A	A	DD	live bait	South America	Júlio-Júnior et al. 2009; Ota et al 2018
Rhamphichthyidae										
Gymnorhamphichthys britskii Carvalho, Ramos & Albert 2011	C	A	A	A	A	A	DD	geographical barrier and live bait	South America	Ota et al. 2018
Gymnorhamphichthys hypostomus Ellis 1912	C	A	A	A	A	A	DD	geographical barrier	South America	Júlio-Júnior et al. 2009
Rhamphichthys hahni (Meinken 1937)	C	A	A	A	A	A	DD	geographical barrier and live bait	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
MYLIOBATIFORMES										
Potamotrygonidae										
Potamotrygon amandae Loboda & Carvalho 2013	E	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Potamotrygon falkneri Castex & Maciel 1963	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
OSTEOGLOSSIFORMES										
Arapaimidae										
Arapaima gigas (Schinz 1822)	D	A	A	A	C	C	DD*	aquaculture	South America	Moraes et al. 2017; Pers. Com. Pessali TC
PERCIFORMES "*sedis mutabilis*"										
Polycentridae										
Polycentrus schomburgkii Müller & Troschel 1849	A	A	A	A	D	A	DD	aquarium trade	South America	Alves et al. 2007; Bartolette et al. 2018
Sciaenidae										
Plagioscion auratus (Castelnau 1855)	A	A	A	A	A	C	DD*	fishing	South America	Barbosa et al. 2017
Plagioscion squamosissimus (Heckel 1840)	E	C	A	A	C	E	DD*	fishing	South America	Teixeira et al 2005; Alves et al. 2007; Langeani et al. 2007; Santos 2010; Rocha et al. 2011; Barros et al. 2012 Sanches et al. 2014; Barbosa et al 2017; Moraes et al. 2017; Ota et al. 2018; Bartolette et al. 2018
PLEURONECTIFORMES										
Achiridae										
Catathyridium jenynsii (Günther 1862)	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al 2009; Ota et al. 2018
SALMONIFORMES										
Salmonidae										
Oncorhynchus mykiss (Walbaum 1792)	D	A	A	A	D	A	DD*	fishing	North America	Bizerril and Primo 2001; Magalhães et al. 2002; Alves et al. 2007; Santos 2010; Casarim et al. 2012

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	**Doce**	**Jequitinhonha**	**Mucuri**	**Paraíba do Sul**	**São Francisco**				
SILURIFORMES										
Ariidae										
Ariopsis seemanni (Günther 1864)	A	A	A	A	C	A	DD	aquarium trade	Central America and South America	Latini et al. 2016
Auchenipteridae										
Ageneiosus inermis (Linnaeus 1766)	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Ageneiosus ucayalensis Castelnau 1855	D	A	A	A	A	A	DD	geographical barrier	South America	Júlio-Júnior et al. 2009; Ota et al. 2018
Auchenipterus osteomystax (Miranda Ribeiro 1918)	E	A	A	A	A	A	DD	geographical barrier	South America	Júlio-Júnior et al. 2009; Ota et al. 2018
Trachelyopterus coriaceus Valenciennes 1840	C	A	A	A	A	A	DD	unknown	South America	Rocha et al. 2011
Trachelyopterus galeatus (Linnaeus 1766)	E	A	A	A	A	N	DD*	geographical barrier	South America	Júlio-Júnior et al. 2009
Callichthyidae										
Hoplosternum littorale (Hancock 1828)	N	E	D	D	D	E	DD*	live bait	South America	Alves et al. 2007; Vieira 2010; Latini et al. 2016; Moraes et al. 2017; Bartolette et al. 2018
Lepthoplosternum pectorale (Boulenger 1895)	C	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Megalechis thoracata (Valenciennes 1840)	C	A	A	A	A	A	DD	live bait	South America	Langeani et al. 2007
Scleromystax barbatus (Quoy & Gaimard 1824)	A	A	A	A	D	A	DD	aquarium trade	South America	Alves et al. 2007
Clariidae										
Clarias gariepinus (Burchell 1822)	D	E	D	D	D	D	DD*	aquaculture	Africa and Asia	Alves et al. 1999; Teixeira et al. 2005; Alves et al. 2007; Langeani et al. 2007; Andrade-Neto 2010; Pompeu 2010; Santos 2010; Vieira 2010; Barbosa et al. 2017; Moraes et al. 2017; Ota et al. 2018

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Doradidae										
Ossancora eigenmanni (Boulenger 1895)	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Platydoras armatulus (Valenciennes 1840)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Pterodoras granulosus (Valenciennes 1821)	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Trachydoras paraguayensis (Eigenmann & Ward 1907)	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Heptapteridae										
Heptapterus mustelinus (Valenciennes 1835)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Ota et al. 2018
Imparfinis longicauda (Boulenger 1887)	C	A	A	A	A	A	DD	unknown	South America	Fagundes et al. 2015
Pimelodella taenioptera Miranda Ribeiro 1914	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Ota et al. 2018
Ictaluridae										
Ictalurus punctatus (Rafinesque 1818)	C	C	A	A	C	A	DD	aquaculture	North America	Alves et al. 2007; Vieira 2010; Ota et al. 2018
Loricariidae										
Ancistrus sp.	A	C	A	A	C	C	DD	aquarium trade	South America	Honorio and Martins 2018; Magalhães et al. 2019
Farlowella hahni Meinken 1937	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Ota et al. 2018
Farlowella oxyrryncha (Kner 1853)	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007
Hypostomus cochliodon Kner 1854	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Hypostomus commersoni Valenciennes 1836	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Hypostomus dlouhyi Weber 1985	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007
Hypostomus microstomus Weber 1987	D	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018

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	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Loricariidae										
Hypostomus ternetzi (Boulenger 1895)	D	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Loricaria simillima Regan 1904	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007
Loricariichthys platymetopon Isbrücker & Nijssen 1979	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Loricariichthys rostratus Reis & Pereira 2000	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Parancistrus aurantiacus (Castelnau 1855)	D	A	A	A	A	A	DD	unknown	South America	Araújo and Tejerina-Garro 2009
Parotocinclus maculicauda (Steindachner 1877)	A	A	A	A	C	A	DD	aquarium trade	South America	Latini et al. 2016
Peckoltia multispinis (Holly 1929)	A	A	A	A	D	A	DD	aquarium trade	South America	Latini et al. 2016
Pogonopoma wertheimeri (Steindachner 1867)	A	D	A	N	A	A	DD	unknown	South America	Alves et al. 2007; Vieira 2010
Pterygoplichthys ambrosettii (Holmberg 1893)	D	D	A	A	A	D	DD	aquarium trade and geographical barrier	South America	Ota et al. 2018; Pers. Com. Pessali TC
Pterygoplichthys joselimaianus (Weber 1991)	C	A	A	A	A	A	DD	unknown	South America	Sanches et al. 2014

Taxon (by Fricke, Eschmeyer & Fong 2020)	Species status in each watershed						Impact	Pathways of introduction	Origin	References
	Upper Paraná	Doce	Jequitinhonha	Mucuri	Paraíba do Sul	São Francisco				
Pimelodidae										
Hypophthalmus oremaculatus Nani & Fuster de Plaza 1947	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Iheringichthys labrosus (Lütken 1874)	E	A	A	A	A	A	DD	unknown	South America	Ota et al. 2018
Pimelodus fur (Lütken 1874)	C	A	A	A	E	N	DD	fishing	South America	Langeani et al. 2007; Santos 2010; Moraes et al. 2017
Pimelodus maculatus Lacepède 1803	N	E	A	A	E	N	DD	fishing	South America	Alves et al. 2007; Vieira 2010; Moraes et al. 2017; Honorio and Martins 2018
Pimelodus ornatus Kner 1858	E	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Pseudoplatystoma corruscans (Spix & Agassiz 1829)	N	A	A	A	C	N	DD	aquaculture	South America	Moraes et al. 2017
Pseudoplatystoma fasciatum x *Pseudoplatystoma corruscans* "hybrid"	C	D	E	C	C	C	DD*	aquaculture	South America	Alves et al. 2007; Andrade-Neto 2010; Vieira 2010
Pseudoplatystoma punctifer x *Leiarius marmoratus* "hybrid"	C	A	A	A	C	A	DD	aquaculture	South America	Sanches et al. 2014; Moraes et al. 2017
Pseudoplatystoma reticulatum Eigenmann & Eigenmann 1889	C	A	A	A	A	A	DD	geographical barrier	South America	Ota et al. 2018
Sorubim lima (Bloch & Schneider 1801)	C	A	A	A	A	A	DD	geographical barrier	South America	Langeani et al. 2007; Júlio-Júnior et al. 2009; Ota et al. 2018
Pseudopimelodidae										
Lophiosilurus alexandri Steindachner 1876	A	E	A	A	C	N	DD	fishing	South America	Bizerril and Primo 2001; Alves et al. 2007; Vieira 2010; Salvador et al. 2018
Trichomycteridae										
Trichomycterus brasiliensis Lütken 1874	C	A	A	A	A	N	DD	unknown	South America	Langeani et al. 2007

References (List of freshwater alien fish species introduced in southeastern Brazil watersheds - Supplementary Material)

Alves CBM, Vieira F, Magalhães ALB, Brito MFG (2007) Impacts of non-native fish species in Minas Gerais, Brazil: present situation and prospects. In: Bert TM (ed) Ecological and Genetic Implications of Aquaculture Activities, 291-314

Alves CBM, Vono V, Vieira F (1999) Presence of the walking catfish *Clarias gariepinus* (Burchell) (Siluriformes, Clariidae) in Minas Gerais state hydrographic basins, Brazil. Rev Bras Zool, 16: 259-263

Andrade-Neto FR (2010) Estado atual do conhecimento sobre a fauna de peixes da bacia do Jequitinhonha. MG. Biota 2 (5): 22-35

Araújo NB, Tejerina-Garro FL (2009) Influence of environmental variables and anthropogenic perturbations on stream fish assemblages, Upper Paraná River, Central Brazil. Neotrop Ichthyol. 7 (1): 31-38

Barbosa JM, Soares EC, Cintra IHA, Hermann M, Araújo ARR (2017) Perfil da ictiofauna da bacia do rio São Francisco. Acta Fish Aquat Res 5 (1): 70-90

Barros LC, Santos U, Zanuncio JC, Dergam JA (2012) *Plagioscion squamosissimus* (Sciaenidae) and *Parachromis managuensis* (Cichlidae): A Threat to Native Fishes of the Doce River in Minas Gerais, Brazil. PLoS One 7(6): e39138. doi:10.1371/journal.pone.0039138

Bartolette R, Lima D, Pacheco ACG, Carvalho A, Peçanha ELS, Souza G, Caramaschi EP (2018) Composição e riqueza de espécies da ictiofauna no domínio das ilhas fluviais da bacia do Rio Paraíba do Sul. In: Berriel TCS, Caramaschi EPC, Polaz CNM (ed) Monitoramento da fauna aquática: funções ecossistêmicas do domínio das ilhas fluviais do Rio Paraíba do Sul. Itaocara, RJ: Projeto Piabanha: 101-129

Bizerril CRSF, Primo PBS (2001) Peixes de águas Interiores do Estado do Rio de Janeiro. Fundação de Estudos do Mar, Rio de Janeiro. 417p.

Carmassi AL, Rondineli G, Ferreira FC, Braga FMS (2012) Composition and structure of fish assemblage from Passa Cinco stream, Corumbataí river sub-basin, SP, Brazil. Braz J Biol 72 (1): 87-96

Casarim R, Bueno ML, Pompeu PS (2012) Ichthyofauna of the Aiuruoca River basin, Minas Gerais, Brazil. Check List 8(6): 1166-1171

Fagundes DC, Leal CG, Carvalho DR, Junqueira NT, Langeani F, Pompeu PS (2015) The stream fish fauna from three regions of the Upper Paraná River basin. Biota Neotrop 15 (2): e20140187

Fricke R, Eschmeyer WN, van der Laan R (2020) Eschmeyer's Catalog of Fishes: Genera, Species, References http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Accessed 10 May 2020

Honorio JR, Martins IA (2018) Ichthyofauna of the Una river in the Paraíba do Sul Paulista River Valley, Southeastern of Brazil. Biota Neotrop 18 (4): e20180528

Júlio-Júnior HF, Dei Tos C, Agostinho AA, Pavanelli CS (2009) A massive invasion of fish species after eliminating a natural barrier in the upper rio Paraná basin. Neotrop Ichthyol. 7 (4):709-18

Langeani F, Castro RMC, Oyakawa OT, Shibatta OA, Pavanelli CS, Casatti L (2007) Diversidade da ictiofauna do Alto Rio Paraná: composição atual e perspectivas futuras. Biota Neotrop 7 (3): 181-197

Langeani F, Rêgo ACL (2014) Guia ilustrado dos peixes da bacia do Rio Araguari. Grupo de Mídia Brasil Central, Uberlândia. 194 p.

Latini AO, Resende DC, Pombo VB, Coradin L (2016) Espécies exóticas invasoras de águas continentais no Brasil. Brasília: MMA. Série Biodiversidade, 39. 791 p.

Magalhães ALB (2007) Novos registros de peixes exóticos para o Estado de Minas Gerais, Brasil. Rev Bras Zool 24 (1): 250-252

Magalhães ALB, Andrade RF, Ratton TF, Brito MFG (2002) Ocorrência da truta arco-íris *Oncorhynchus mykiss* (Walbaum, 1792) (Pisces: Salmonidae) no alto rio Aiuruoca e tributários, bacia do rio Grande, Minas Gerais, Brasil. Bol Mus Biol Mello Leitão. 14: 33-40

Magalhães ALB, Azevedo-Santos VM, Lima-Júnior DP, Brito MFG (2016) "Por fora bela viola, por dentro pão bolorento": invasões biológicas na lagoa da Pampulha como desafio para o novo Patrimônio Mundial da Humanidade. Boletim ABLimno. 42 (2): 25-33

Magalhães ALB, Brito MFG, Sarrouh B (2019) An inconvenient routine: introduction, establishment and spread of new non-native fishes in the Paraíba do Sul River basin, state of Minas Gerais, Brazil. Neotrop Biol Conserv 14 (3): 329-338

Magalhães ALB, Carvalho PA (2007) Occurrence of exotic ornamental fish in streams in the states of Minas Gerais and Rio de Janeiro, Brazil. Nat Conserv 5 (2): 124-129

Magalhães ALB, Jacobi CM (2008) Ornamental exotic fish introduced into Atlantic Forest water bodies, Brazil. Neotrop Biol Conserv 3 (2): 73-77

Magalhães ALB, Jacobi CM (2013) Asian aquarium fishes in a Neotropical biodiversity hotspot: impeding establishment, spread and impacts. Biol Invas 15(10), 2157–2163

Magalhães ALB, Jacobi CM (2017) Colorful invasion in permissive Neotropical ecosystems: establishment of ornamental non-native poeciliids of the genera *Poecilia/Xiphophorus* (Cyprinodontiformes: Poeciliidae) and management alternatives. Neotrop Ichthyol 15 (1): e160094

Magalhães ALB, Ratton TF (2005) Reproduction of a South American population of pumpkinseed sunfish *Lepomis gibbosus* (Linnaeus) (Osteichthyes, Centrarchidae): a comparison with the European and North American populations. Rev Bras Zool 22 (2): 477-483

Moraes MB, Polaz CNM, Caramaschi EP, Santos-Júnior S, Souza G, Carvalho FL (2017) Espécies Exóticas e Alóctones da Bacia do Rio Paraíba do Sul: Implicações para a Conservação. In: Polaz CNM, Ribeiro KT, Oliveto FA (ed) Conservação de peixes continentais e manejo de unidades de conservação. Biodiv Bras 7 (1): 35-55

Moreira-Filho O; Margarido VP, Bellafronte E, Peres WAM, Kantek DLZ, Pádua K, Blanco DR, Buckup PA, Giuliano-Caetano e Rocha O (2006) Caracterização de espécies de peixes do rio Grande, transpostas para a bacia do rio São Francisco. XXVI Congresso Brasileiro de Zoologia. Sociedade Brasileira de Zoologia, Universidade Estadual de Londrina - PR

Ota RR, Deprá GC, Graça WJ, Pavanelli CS (2018) Peixes da planície de inundação do alto rio Paraná e áreas adjacentes: revised, annotated and updated. Neotrop Ichthyol 16 (2): e170094

Oyakawa OT, Menezes NA (2011) Checklist dos peixes de água doce do Estado de São Paulo, Brasil. Biota Neotrop 11 (1a): 000-000

Pompeu PS, Alves CBM (2003) Local fish extinction in a small tropical lake in Brazil. Neotrop Ichthyol 1 (2): 133–135

Pompeu PS (2010) Os peixes do rio Mucuri. MG. Biota 2 (5): 36-43

Pugedo ML, Andrade-Neto FR, Pessali TC, Birindelli JLO, Carvalho DC (2016) Integrative taxonomy supports new candidate fish species in a poorly studied neotropical region: The Jequitinhonha River Basin. Genetica doi 10.1007/s10709-016-9903-4

Ribeiro MD, Teresa FB, Casatti L (2016) Use of functional traits to assess changes in stream fish assemblages across a habitat gradient. Neotrop Ichthyol 14 (1): e140185

Roa-Fuentes C, Zeni JO, Varella HR, Langeani F, Molina MC (2015) First record of *Crenicichla semifasciata* (Heckel, 1840) (Teleostei: Cichlidae) in the upper Rio Paraná basin, Brazil. Check List 11(2): 1610

Rocha O, Espíndola ELG, Rietzler AC, Fenerich-Verani N, Verani JR (2011) Animal invaders in São Paulo state reservoirs. Oecologia Australis 15 (3): 631-642

Salgado FLK, Terra BF, Camilo GS, Silva EO, Araujo FG (2015) Occurrence of *Pseudocorynopoma heterandria* Eigenmann, 1914 (Characidae) in Paraıba do Sul River Basin (Southeastern Brazil). J Appl Ichthyol 31: 390-392

Salgado FLK, Terra BF, Camilo GS, Araújo FG (2017) First record of the family Parodontidae (Characiformes) from the Paraíba do Sul river basin, southeastern Brazil. Check List 13 (6): 1091-1095. https://doi.org/10.15560/13.6.1091

Salvador GN, Frederico RG, Pessali TC, Vieira F, Freitas TMS (2018) Length-weight relationship of 21 fish species from Rio Doce River basin, Minas Gerais, Brazil. J Appl Ichthyol 00:1-4. https://doi.org/10.1111/jai.13734

Sampaio WMS, Belei F, Giongo P, Dergam JA, Orsi ML (2017) *Heterotilapia buttikoferi* (Hubrecht, 1881) (Perciformes: Cichlidae), an introduced exotic fish in the upper Paraná river basin. Check List 13 (4): 245-250

Sanches BO, Becker B, Gomes PLA, Santos GB (2014) A ictiofauna de quatro reservatórios da CEMIG: caracterização das comunidades. In: Callisto M, Alves CBM, Lopes JM, Castro MA (ed) Condições ecológicas em bacias hidrográficas de empreendimentos hidrelétricos. Belo Horizonte: Companhia Energética de Minas Gerais 1 (2): 185-214

Santos GB (2010) A ictiofauna da bacia do Alto Paraná (rio Grande e rio Paranaíba). MG. Biota 2 (6): 5-25

Santos JAP, Esteves KE (2014) The fish fauna of an Atlantic Forest conservation area in the largest urban center of South America (São Paulo, SP, Brazil) and its relationship to some environmental factors. Stud Neotrop Fauna Environ 49 (2): 135-150

Teixeira TP, Pinto BCT, Terra BF, Estiliano EO, Gracia D, Araújo FG (2005) Diversidade das assembleias de peixes nas quatro unidades geográficas do rio Paraíba do Sul. Iheringia 95(4): 347-357

Vieira F, Rodrigues RR (2010) A fauna de peixes dos afluentes do rio Paraíba do Sul no estado de Minas Gerais. MG. Biota 3 (1): 5-23

Vieira F (2010) Distribuição, impactos ambientais e conservação da fauna de peixes da bacia do rio Doce. MG. Biota 2 (5): 5-22

ARTIGO II

Physical habitat variables importance in the presence and abundance of a globally invasive fish

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Physical habitat variables importance in the presence and abundance of a globally invasive fish

Abstract

The stream habitat comprises all biotic and abiotic variables that influence or provide sustenance to aquatic biota. Changes in physical habitat characteristics associated with anthropogenic disturbances can benefit the establishment and expansion of exotic species in receiving environments. Here, we aimed to evaluate the relative importance of physical habitat variables for the presence and abundance of the invasive fish *Poecilia reticulata*. We sampled fish species and assessed environmental variables through a physical habitat protocol in 231 streams located in southeastern and midwestern Brazil. This protocol measured 258 variables that describe the physical characteristics of streams. We therefore implemented dimensionality reduction methods to limit redundancy, resulting in a smaller set containing the most representative variables. Subsequently, we used two random forest models to assess the relative importance of these variables for the presence and abundance of *P. reticulata*. The presence of this invasive fish in the sampled streams was mainly explained by human disturbance variables related to urbanization (total impact, trash and landfill, pipes, influent and effluent, and pavement), whereas the channel morphology (mean bank full height and mean bank full depth) and fish cover (natural fish cover and aquatic macrophyte areal cover) variables were important predictors for the abundance of this species at the sites where it was introduced. Identifying which habitat variables are favorable to the establishment of exotic species is an important step in preventing future biological invasions, as well as managing those that have already taken place.

Keywords: Guppy, alien species, urbanization, physical habitat, stream.

Resumo

O habitat dos riachos compreende todas as variáveis bióticas e abióticas que influenciam ou fornecem sustento à biota aquática. Mudanças nas características do habitat físico, juntamente com as perturbações antrópicas, podem favorecer o estabelecimento e expansão de espécies exóticas nos ambientes receptores. Portanto, o objetivo do nosso trabalho foi avaliar a importância relativa de variáveis de habitat físico na presença e abundância do peixe exótico invasor *Poecilia reticulata*. Para isso, nosso estudo foi realizado em 231 riachos localizados no sudeste e centro-oeste do Brasil, onde realizamos coleta de peixes e acessamos variáveis ambientais através de um protocolo de habitat físico. O protocolo produz 258 variáveis que descrevem as características físicas dos riachos. Assim, um processo de redução da dimensão dos dados foi conduzido a fim de limitar a redundância e produzir um conjunto menor com as variáveis mais representativas. Em seguida, nós utilizamos dois modelos de random forest para acessar a importância relativa dessas variáveis na presença e abundância de *P. reticulata*. A presença deste peixe invasor nos riachos amostrados foi explicada principalmente pelas variáveis de distúrbio humano relacionadas à urbanização (impacto total, lixo e aterro, tubulações, afluente e efluente, e pavimento), enquanto as variáveis de morfologia do canal (altura do leito sazonal e profundidade do leito sazonal) e abrigo para peixes (abrigo natural e macrófitas) foram importantes para determinar se esta espécie será abundante nos locais onde foi introduzida. Identificar quais variáveis do habitat são favoráveis ao estabelecimento de espécies exóticas é um passo importante para prevenir futuras invasões biológicas, bem como manejar aquelas que já aconteceram.

Palavras-chave: Guppy, espécies exóticas, urbanização, habitat físico, riacho.

1. Introduction

Human activities profoundly affect the global environment (Lewis and Maslin 2015), causing the degradation of natural ecosystem functions and services and consequently favoring biological invasions (Pelicice et al. 2021). For centuries, people have transported and introduced species outside their native ranges for a variety of reasons (Seebens et al. 2018; Bueno et al. 2021). However, the risk of biological invasions is increasing rapidly worldwide due to globalization, technological advancements, and the growth of the human population (Ricciard et al. 2017; Pyšek et al. 2020). Invasive species affect the functioning of ecosystems, and these impacts threaten native biodiversity, human health, and the economy (Ricciardi et al. 2017; Adelino et al. 2021; Reynolds and Aldridge 2021; Vilà et al. 2021). The impacts of invasive species tend to increase over time in all habitat types (Leão et al. 2011); however, they are especially large in island and freshwater ecosystems (IPBES 2019). Freshwater systems are among the most threatened and invaded ecosystems in the world (Leprieur et al. 2008; Garcia et al. 2021), and fish are one of the most introduced species (Seebens et al. 2017). South America's freshwater ecosystems, for example, are threatened by several invasive species and other anthropogenic stressors, in addition to lacking adequate legislation for environmental conservation (Pelicice et al. 2017; Torremorell et al. 2021). Anthropogenic disturbances facilitate the introduction and dispersal of alien species by increasing propagule pressure; therefore, the number of alien species tends to be higher in areas that are more populated, environmentally degraded and economically developed (Dias et al. 2020; Guimarães Silva et al. 2020). A greater number of freshwater fish introductions may occur in more densely populated regions (Dawson et al. 2017), as has been reported in Brazil, where 201 alien fish species have been introduced in the main watersheds of a region with high human population density (Bueno et al. 2021).

The guppy (*Poecilia reticulata* Peters, 1859) is a fish species native to Venezuela, Barbados, Trinidad, northern Brazil and the Guianas that has been widely introduced and established throughout temperate and tropical freshwater systems worldwide, mainly due to the aquarium trade or for biological control (CABI 2021; Froese and Pauly 2021). While *P. reticulata* is native to northern Brazil, it has also been introduced to many Brazilian watersheds, and it is currently widely distributed in the country (Bueno et al. 2021; Base de Dados Nacional de Espécies Exóticas Invasoras 2021). *Poecilia reticulata* is an opportunistic species able to tolerate degraded environments (Cassati et al. 2009; de Carvalho et al. 2019). This livebearing alien fish species is omnivorous, feeding on algae, invertebrate larvae and benthic detritus (CABI 2021), and can also consume sewage, which may facilitate its establishment in polluted sites (de Carvalho et al. 2019). Furthermore, other guppy characteristics, such as sperm storage and early reproductive maturity, may increase the success of establishment and invasion in recipient streams and, consequently, the species' potential impacts on native biota (Dias et al. 2020).

Physical habitat characteristics are important drivers of the structure and richness of ichthyofauna; therefore, changes in stream environments can also influence biological invasions (Cruz and Pompeu 2020; Peressin et al. 2020). Alterations in riparian vegetation, habitat complexity, channel morphology, and water quality can directly affect native biota, possibly benefiting alien species (Casatti et al. 2009; Cruz and Pompeu 2020). For instance, *P. reticulata* was the species which caused the most dissimilarity in the ichthyofauna structure between less and more disturbed streams in southeastern Brazil (Casatti et al. 2006), and it is associated to a poor biotic integrity (de Carvalho et al. 2017b). Furthermore, the density of *P. reticulata* populations tends to be higher in urban streams (Marques et al. 2020), indicating that habitat simplification could increase this species' chance of establishment and invasion in freshwater environments. Therefore, given this species' wide distribution, life history traits, and environmental impacts, understanding how physical factors influence its invasion is extremely important.

Habitat alterations from anthropogenic disturbances play an important role in the invasiveness of a species (Guimarães Silva 2020). Such processes are of particular concern in freshwater systems since they may result in dramatic changes to native communities by reducing or eliminating native competitors and predators, increasing watershed connectivity, or increasing habitat homogenization, which may provide new vacant niches for the most opportunistic invaders (Gherardi 2007; Ricciardi and MacIsaac 2011; Alexander et al. 2015). Given the current scenario of increasing habitat degradation and biological invasions, the aim of our study was to evaluate the relative importance of physical habitat variables of streams for the presence and abundance of the invasive fish *P. reticulata*. Our study utilized a large network of 231 streams in Brazil. *P. reticulata* is a known bioindicator of poor water quality and is associated with disturbed environments (Pinto & Araújo 2007; de Carvalho et al. 2017b; Dias et al. 2020), but it remains unknown which physical variables of streams affect their presence and abundance. By improving our knowledge of how the physical environment is related to biological invasions, we provide a basis for a greater understanding of the invasion process and for improving the management of alien species and preventing future introductions.

2. Methods

2.1 Study area

We studied 231 stream sites with different conditions of biotic integrity and ranging from 1st to 3rd Strahler order on a digital 1:100,000 scale map (Strahler, 1957). We sampled both streams minimally disturbed by human activities, which possess characteristics representative of the region where they are located, and severely disturbed streams (e.g., urban streams). All streams belonged to the Paraná (165 stream sites) or São Francisco (66 stream sites) river basins in the Brazilian states of Minas Gerais and São Paulo (Southeast) and Goiás (Midwest) (Fig. 1). The streams were randomly selected for sampling using a Generalized Random-Tessellation Stratified (GRTS) design, after standardizing the order, width, and depth dimensions of the water bodies (Macedo et al. 2014).

The Paraná River basin drains approximately 10% of the Brazilian territory (879,860 km^2) and is the second largest watershed in the country (Zandonadi et al. 2016). The São Francisco River basin drains approximately 8% of the Brazilian territory (645,000 km^2) (de Carvalho et al. 2017b; Bueno et al. 2021 and references therein). These watersheds drain one of the most economically developed regions of Brazil and are highly impacted by alien species, land-use changes, pollution, and other anthropogenic stressors (Bueno et al. 2021).

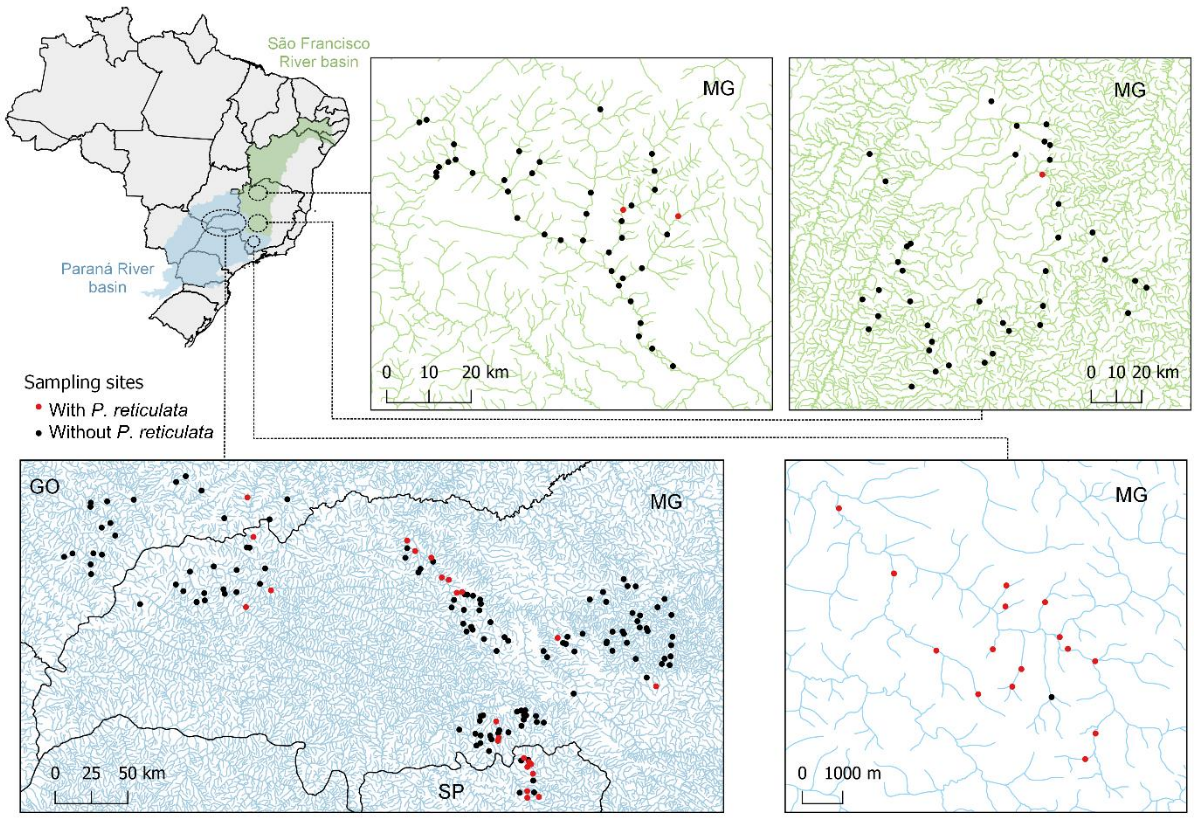

Fig. 1 Sampling sites distributed in the São Francisco (green hydrography) and Paraná (blue hydrography) River basins, in the Brazilian states of Minas Gerais (MG), São Paulo (SP), and Goiás (GO). Red dots represent stream sites with *Poecilia reticulata*.

2.2 Data sampling

Each stream site was sampled only once, between 2009 and 2019, during the dry season. The length of the sampled stretch in each stream was proportional to its width, defined by multiplying the average width of the stream by 40, and had a minimum stretch of 150 m (Kaufmann et al. 1999; Peck et al. 2006; Hughes and Peck, 2008). For fish sampling and characterization of physical habitats, the stretch was divided into 10 sections separated by 11 cross-sectional transects (A-K) (Macedo et al. 2014).

2.2.1 Fish sampling

In each section, two people sampled fish using semicircular hand nets (80 cm diameter, 1 mm mesh) and seines (4 m long, 2 m high, 5 mm mesh) when possible (de Carvalho et al. 2017b). Each section was sampled for 12 minutes, for a total of two daylight hours in each stream (Junqueira 2011; de Carvalho et al. 2017b). The specimens were killed with an anesthetic solution of eugenol, labeled according to section and fixed in a 10% formalin solution. The collected material was transported to the Fish Ecology Laboratory (UFLA), where it was transferred to a 70% alcohol solution. Afterward, the fishes were identified to the species level.

2.2.2 Physical habitat characterization

Physical habitat variables were assessed at all sites using the physical habitat assessment protocol proposed by Peck et al. (2006) and Hughes and Peck (2008). The main groups of variables evaluated were channel dimensions, longitudinal gradient and sinuosity, substrate types, in-channel cover, riparian vegetation, interactions between the surroundings and the channel structure, and human disturbance. For each section, we measured the thalweg depth, the presence of fine substrate, channel bars, backwaters, side channels, and the channel type. We also measured the channel slope and sinuosity through compass bearings. For each transect, we measured depth and made visual observations to assess the substrate types and their immersion. The bank full width and depth, wetted width and mean depth, incision height, undercut bank distance, and bank angle were determined. The available fish cover was estimated visually in 10 m^2 plots inside the stream channel. We measured the vegetation canopy cover above the channel with a densitometer and the riparian vegetation types with visual estimates. We also assessed the frequency and extent of both in-channel and near-channel human activities and disturbances. From the data collected using the physical habitat protocol, it was possible to calculate the metrics (condensed values of the observations) for each stream (de Carvalho et al. 2017a). The following water quality variables were also measured at each site: the dissolved oxygen (mg/L), pH, temperature (°C), electrical conductivity (µS/cm), turbidity (UNT), total dissolved solids (mg/L), and dissolved nitrogen (mg/L).

2.3 Explanatory variables reduction

The physical habitat assessment protocol produces a list of 258 variables that describe the physical characteristics of streams. Furthermore, we include the variables of water quality for each stream and sampling region (site). Therefore, a process of reducing the number of variables was conducted in order to limit redundancy and produce a smaller set of the most representative variables (Leal et al. 2016; Cruz and Pompeu 2020) (Fig. 2). Firstly, we used our specialist judgment to remove variables that were not relevant to our study. Secondly, we removed variables with missing values, and zero or near zero-variance predictors. Next, we excluded correlated variables ($\rho_{Spearman} > 0.5$), considering the pair-wise correlations and keeping one of the variables with the highest biological representation (using *corrplot* package – Wei and Simko 2021; R Core Team 2021). Finally, a principal component analysis (PCA) was conducted for each group of physical habitat variables (channel morphology, substrate, channel flow, riparian vegetation cover, fish cover, and human disturbance) (*FactoMineR* package – Le et al. 2008; R Core Team 2021). We used the *paran* package, which performs Horn's parallel analysis for evaluating the components retained in a PCA (Dinno 2018; R Core Team 2021), to determine the number of dimensions to extract. By inspecting the contribution of variables of the axis retained after Horn's parallel analysis, we obtained the variables with contribution values higher than the mean and used them in the final dataset (the variable reduction process is visually detailed in Fig. 2). The plot with the contribution of variables was constructed using *fviz_contrib* function in *factoextra* package (Kassambara and Mundt 2020; R Core Team 2021).

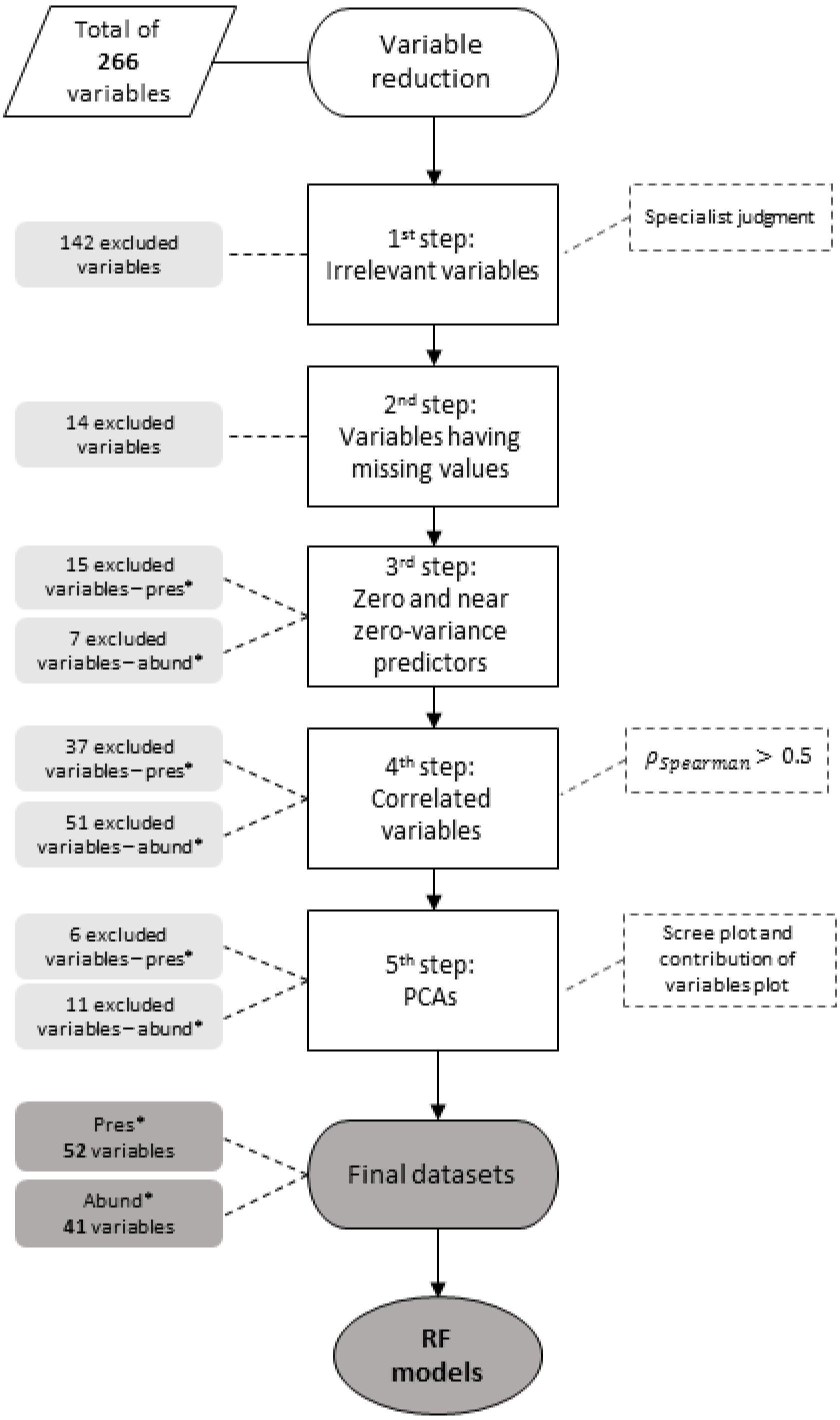

Fig. 2 Diagram showing the variable reduction criteria for building random forest models (RF). In the first and second steps, the excluded variables were the same for the two RF models. From the third step onwards, the excluded variables were different in each model. The complete list of variables used in RF models is available in the Table 1. 'Pres' = model with data of presence of *Poecilia reticulata*; 'Abund' = model with data of abundance of *P. reticulata*; 'PCAs' = principal component analyses.

2.4 Data analysis

We used two random forest (RF) models (Breiman 2001) to assess the relative importance of the retained physical habitat variables for both the presence and abundance of the invasive fish *P. reticulata* in Brazilian streams. Random forests are machine learning algorithms that combine many decision trees to produce more accurate classifications. They are an effective method of determining the importance of variables due to their high classification accuracy and their ability to model complex interactions among predictor variables (Cutler et al. 2007). Using the *randomForest* package (Liaw and Wiener 2002; R Core Team 2021), we built two RF models with data on the presence (data drawn from all sampled streams) and abundance (data drawn from streams where the invasive fish were sampled) of *P. reticulata*. We fitted two important parameters in the RF models: the number of trees used in the forest (*ntree* = 1000) and the number of variables randomly sampled as candidates at each split in each tree (the optimal *mtry* value). The optimal *mtry* value was found for each model by using the *tuneRF* function from the *randomForest* package (Liaw and Wiener 2002; R Core Team 2021). Using this procedure, we obtained the most important variables and built partial dependence plots to graphically demonstrate both the relationships between individual predictor variables and the predicted probabilities of *P. reticulata* presence and abundance obtained from the RF models (Cutler et al. 2007). Partial dependence provides a quantitative depiction of the relationship between the outcome and the predictors as detected by the RF model (Jones and Linder 2015).

3. Results

3.1 Variable selection

The variable selection process resulted in the exclusion of 142 variables that were irrelevant to our study and 14 variables with missing values. In the presence/absence model, 15 zero- and near-zero-variance predictors and 37 correlated variables were excluded. After performing the PCAs and obtaining the most relevant variables, 52 variables remained in the final dataset for building the RF. In the abundance model, dimensionality reduction resulted in the exclusion of seven zero- and near zero-variance predictors and 51 correlated variables. The final dataset to build the RF contained the 41 variables obtained through the PCAs (Table 1).

Table 1 The final datasets with the variables used in two randon forest models. 'Pres' = model with data of presence of *Poecilia reticulata*; 'Abund' = model with data of abundance of *P. reticulata*.

Variable	Description	Model
	Identification Variables	
SITE	Watershed	Pres; Abund
	Channel Morphology Metrics	
XDEPTH_T	Mean thalweg depth (cm)	Pres
XWIDTH	Mean wetted width (m)	Pres; Abund
PCT_FA	Percent falls	Abund
PCT_RA	Percent rapids	Pres; Abund
PCT_RI	Percent riffle	Pres; Abund
PCT_GL	Percent glide	Pres
PCT_PD	Percent impoundment pool	Pres
PCT_PL	Percent lateral scour pool	Abund
PCT_SB	Percent subsurface flow	Pres; Abund
PCT_SLOW	Percent glides + all pool types	Pres; Abund
PCT_POOL	Percent all pool types	Pres; Abund
SEQ_FLO_1	Sequence - rapids, glides and pools	Pres
	Channel Cross-section and Bank Morphology Metrics	
XBKA	Mean bank angle (degrees)	Pres
XUN	Mean bank undercut distance (m)	Abund
XBKF_W	Mean bank full width (m)	Pres
XBKF_D	Mean bank full depth (m)	Pres; Abund
XBKF_H	Mean bank full height (m)	Pres; Abund
XBAR	Mean channel bars width (m)	Abund
	Channel Sinuosity and Slope Metrics	
SINU	Channel Sinuosity = Reach length / Straight line distance between reach ends)	Pres; Abund
	Residual Pool Metrics	
PCTRSED	Presence of thalweg small sediments (% of reach length)	Pres
	Substrate Size and Composition Metrics	
PCT_RR	Substrate % rough bedrock (>4000mm)	Abund
PCT_BL	Substrate % boulder(250-4000mm)	Abund
PCT_CB	Substrate % cobble (64-250mm)	Pres
PCT_GC	Substrate % coarse gravel (16-64mm)	Pres
PCT_BIGR	Substrate % coarse gravel and larger (>16mm)	Pres; Abund
PCT_GF	Substrate % fine gravel (2-16mm)	Pres; Abund
PCT_SA	Substrate % sand (0 6-2mm)	Pres
PCT_FN	Substrate % fine (silt/clay < 0 6 mm)	Pres; Abund
PCT_SAFN	Substrate % sand + fines (<2mm)	Abund
PCT_WD	Substrate % wood	Pres; Abund
PCT_ORG	Substrate % wood or detritus	Pres; Abund
PCT_HP	Substrate % hard pan	Pres; Abund
PCT_OT	Substrate % miscellaneous other types	Pres

Variable	Description	Model
Substrate Size and Composition Metrics		
PCT_RT	Substrate % roots	Pres
PCT_SF	Substrate % fine litter	Pres; Abund
PCT_ALMA	Substrate % algae + macrophytes	Abund
Fish Cover Metrics		
XFC_ALG	Filamentous algae areal cover	Pres
XFC_AQM	Aquatic macrophyte areal cover	Pres; Abund
XFC_LWD	Large woody debris areal cover	Pres; Abund
XFC_OHV	Overhanging vegetation areal cover	Pres; Abund
XFC_HUM	Artificial structure areal cover	Abund
XFC_LIF	Sum of proportional areal cover from natural concealment features, including leaf bank and living roots	Pres; Abund
XFC_ANT	Anthropogenic fish cover areal cover	Pres; Abund
XFC_WD	Woody debris areal cover	Pres
Riparian Cover (Densiometer) Metrics		
XCDENBK	Mean % canopy density at bank	Pres
XCDENMID	Mean % canopy density mid-stream	Pres; Abund
Riparian Vegetation Cover and Structure Metrics		
XCL	Riparian canopy (> 5 m high) cover - trees > 0.3m DBH	Pres
XGW	Riparian ground-layer (< 0.5 m high) woody cover	Pres
XGH	Riparian ground-layer (< 0.5 m high) herbaceous cover	Pres; Abund
XC	Riparian canopy cover (XCL+XCS)	Pres
XG	Riparian ground-layer vegetation cover (XGW + XGH)	Pres; Abund
Human Disturbance Metric Variables		
W1H_WALL	Channel revetment (proximity-weighted index)	
W1H_PVMT	Pavement (proximity-weighted index)	Pres
W1H_PIPE	Pipes, influent and effluent (proximity-weighted index)	Pres; Abund
W1H_LDFL	Trash and Landfill (proximity-weighted index)	Pres; Abund
W1H_CROP	Row Crop Agriculture (proximity-weighted index)	Pres
W1H_PSTR	Pasture and Grass fields (proximity-weighted index)	Abund
W1H_LOG	Logging (proximity-weighted index)	Pres
W1_HALL	Riparian human disturbance index – All types (proximity-weighted sum index)	Pres; Abund
W1_HAG	Agricultural types (proximity-weighted sum index)	Abund
X_HALL	Proportion of human impact per stretch - Total (margin + < 10m + > 10m) (B+C+P)	Abund
X_HAG	Proportion of agricultural human impact per stretch - Total (margin + < 10m + > 10m) (B+C+P)	Pres
Water quality variables		
COND	Electrical conductivity (µS/cm)	Pres; Abund

3.2 *Poecilia reticulata* invasion

A total of 14,816 *P. reticulata* individuals were collected in 43 of the 231 stream sites. The mean number of individuals collected per stream was 345 (range: 1-6,909 individuals/stream). The streams where the guppies were collected had some degree of disturbance and most were located near or within urban areas. A high abundance of guppies was recorded in the Paraná River basin, with the invasive species found in 24% of the sampled streams in this watershed. Conversely, a lower presence and abundance of guppies was recorded in the São Francisco River basin.

The predictor variables and their percentages of explanation varied between the two RF models (Fig. 3). In the presence/absence RF model (out-of-bag error = 0.11; area under the ROC curve (AUC) = 0.76), the presence of *P. reticulata* was explained mainly by human disturbance. Four of the five most important variables in the model were human disturbance variables: total impact (proximity-weighted sum) (mean decrease in accuracy (%IncMSE) = 16.02%), trash and landfill (proximity-weighted index) (%IncMSE = 14.63%), pipes, influent and effluent (proximity-weighted index) (%IncMSE = 9.66%), and pavement (proximity-weighted index) (%IncMSE = 8.61%). Specific predictor variables – total impact, trash and landfill, pipes, influent and effluent, and pavement – were positively related with the presence of *P. reticulata* (Fig. 4).

In the abundance RF model (% variance explained = 17.69; R^2 = 0.83), the instream variables better explained guppy abundance, as the most important predictors were mean bank full height (m) (%IncMSE = 7.63%); natural fish cover, including leaf bank and living roots (sum of proportional areal cover from natural concealment features) (%IncMSE = 6.98%); mean bank full depth (m) (%IncMSE = 5.93%); and aquatic macrophyte areal cover (%IncMSE = 5.61%). Specific predictor variables – mean bank full height, natural fish cover, mean bank full depth, and aquatic macrophyte areal cover – were positively related with the abundance of *P. reticulata* (Fig. 5).

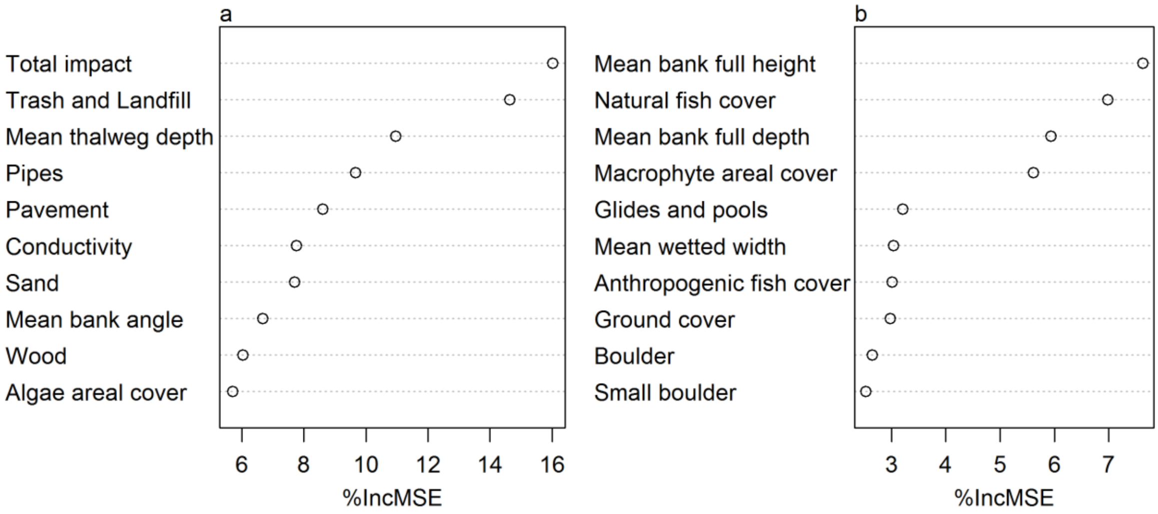

Fig. 3 Variable importance plots for predictor variables from the random forest models for predicting presence (a), and abundance (b) of *Poecilia reticulata* in Brazilian streams. Higher values of mean decrease in accuracy (%IncMSE) indicate higher importance of predictor variables.

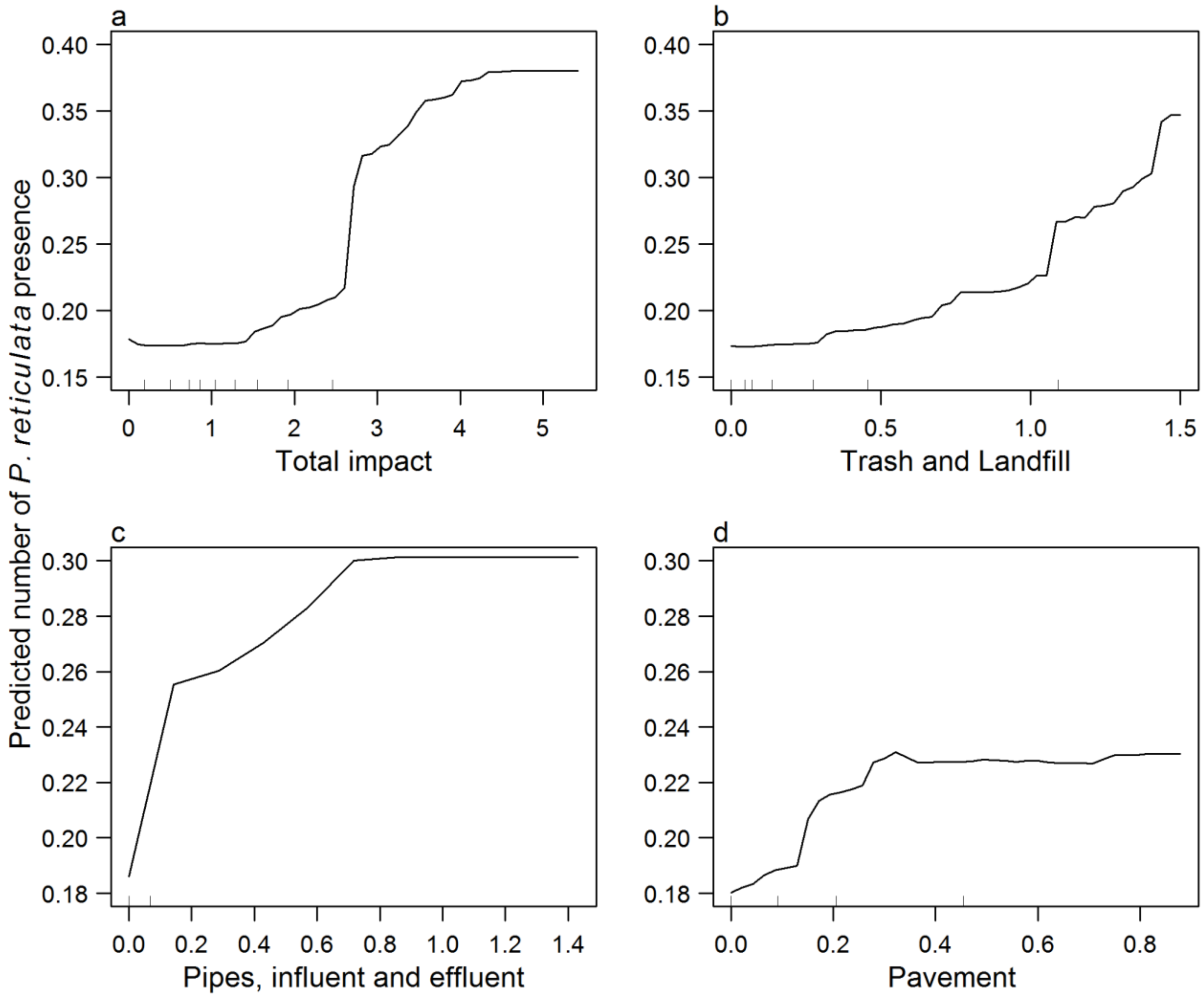

Fig. 4 Partial dependence plots for selected predictor variables for random forest predictions of *Poecilia reticulata* presence in Brazilian streams. The human disturbance metric variables were calculated by riparian human disturbance index: a) total impact = proximity-weighted sum; b) trash and landfill = proximity-weighted index; c) pipes, influent and effluent = proximity-weighted index; d) pavement = proximity-weighted index. Human disturbances indexes were calculated according Kauffman et al. 1999 and Peck, 2006. The tick marks on the x-axis indicate the min/max and deciles of the predictor distributions.

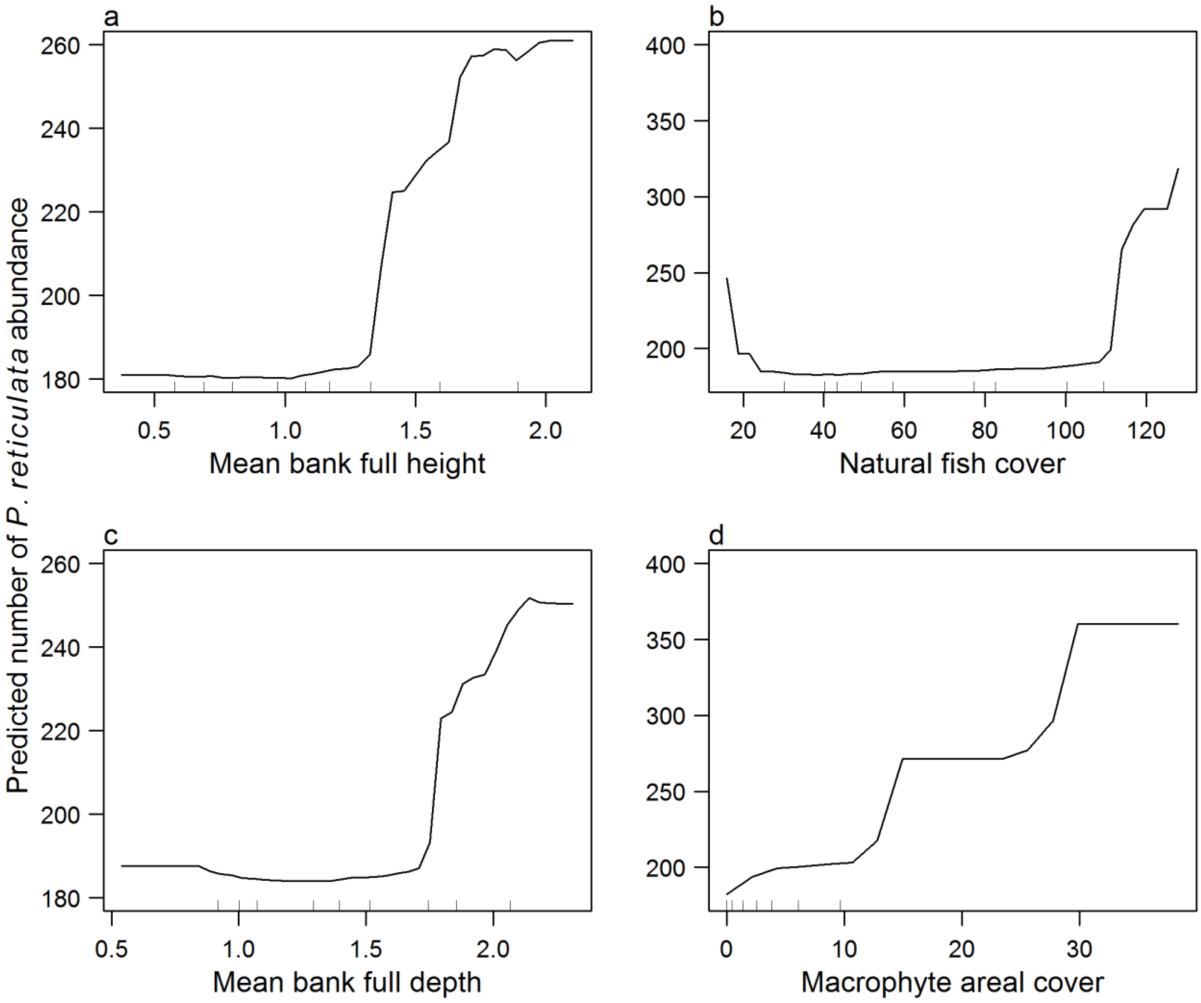

Fig. 5 Partial dependence plots for selected predictor variables for random forest predictions of *Poecilia reticulata* abundance in Brazilian streams. The channel morphology metrics (a; c) were measured in meters (m), and the fish cover metrics were measured by the percentage of areal cover of each features type: b) natural fish cover types (sum of proportional areal cover from natural concealment features: rocks and boulders, overhanging vegetation, brush, large woody debris, and undercut banks. The code calculates cover estimates of these combined cover types, whose summed cover may exceed 100%, i.e., proportional areal cover > 1.0); d) aquatic macrophyte areal cover proportion (see Kauffman et al. 1999). The tick marks on the x-axis indicate the min/max and deciles of the predictor distributions.

4. Discussion

We identified which physical habitat variables were important in predicting the presence and abundance of the globally invasive fish *P. reticulata*. Our results demonstrated that human disturbance variables are important drivers of *P. reticulata* presence, while instream variables, mainly those related to channel morphology and fish cover, are important drivers of its abundance. The expansion of human activities has modified the structure, dynamics, history, and function of freshwater ecosystems (Pelicice et al. 2021). Simplified and disturbed habitats tend to favor alien species, which are more tolerant of human-modified conditions and have traits that enable them to persist in sites where native species are not able to (Casatti et al. 2006). These problems are accentuated in stream ecosystems, as they are small-scale environments that are extremely sensitive to human disturbance (Garcia et al. 2021). Therefore, our results reinforce the importance of protecting the biotic integrity of watercourses to manage and prevent biological invasions.

The human disturbance variables that predict *P. reticulata* presence (total impact, trash and landfill, pipes, influent and effluent, and pavement) are highly related to urbanization. Urbanization can transform the environment in drastic ways (Marques et al. 2020); for example, with increasing urbanization, natural areas are replaced by built structures and water and air pollution increase. Urban areas create distinct environmental conditions that benefit tolerant generalist taxa and reduce sensitive specialized taxa (Marques et al. 2020; Borden and Flory 2021). *Poecilia reticulata* is a tolerant species that can establish at sites that are disturbed, are highly polluted, and have poor water quality (de Carvalho et al. 2019; Gomes-Silva et al. 2020); thus, this alien species is commonly found in urban streams (Cruz and Pompeu 2020), confirming importance of human disturbance variables on its presence. Furthermore, the guppy’s dietary flexibility is an important trait for surviving and flourishing in urban areas, since this alien species has the potential to compete with native biota in a wide range of conditions and resources (Ganassin et al. 2019). For example, guppies can assimilate carbon directly from sewage, which can facilitate their establishment in urban areas (de Carvalho et al. 2019).

Paved roads are also a key urbanization indicator that strongly affect freshwater environments across large spatial and temporal frames (Angermeier et al. 2004; Cui and Shi 2012). In human history, roads were one of the first ways of overcoming biogeographic barriers and connecting areas (Nentwig 2008); currently, they are relevant predictors for explaining the occurrence of certain alien species in disturbed environments (Gallardo 2014). In addition to their impacts to stream habitat characteristics (Leal et al. 2016) and their biota (Angermeier et al. 2004), paved roads are important pathways for the introduction of alien fish species (Dias et al. 2020). These invasion routes also occur in terrestrial environments, where roads favor the dispersal and establishment of alien plants in new landscapes or regions (Guimarães Silva et al. 2020). Roads facilitate people's access to water bodies and, consequently, increase the chances of guppy release in urban streams (Dias et al. 2020), both for mosquito control and for disposal from the aquarium trade (Warbanski et al. 2017; Bueno et al. 2021). Therefore, urban environments tend to be points of introduction for *P. reticulata* as well as important hotspots for the entry of many alien species, which often flourish and become invasive in these areas (Marques et al. 2020; Borden and Flory 2021).

Once introduced in disturbed areas, *P. reticulata* often becomes numerically dominant (Dias et al. 2020), enhancing its invasive potential (Marques et al. 2020). Our results showed that there was a positive relationship between *P. reticulata* abundance and channel morphology variables (mean bank full height and mean bank full depth). This relationship may also be related to urbanization, as urban streams tend to have deep, wide, and slow channels (Angermeier et al. 2004). Guppies can occur in a wide range of habitats, but they are commonly found in shallow stream margins (CABI 2021). However, it has been reported that larger individuals are more likely to remain in deeper and more central and areas and that guppies select shallow water when predatory fish are present (Meffe and Snelson 1989, and references therein). This is consistent with our results, as there is evidence that urban guppies have larger body sizes (Marques et al. 2020) and are thus able to occupy deeper waters. Furthermore, there is biotic homogenization in environments where invasive guppies are dominant (Cruz and Pompeu 2020), reducing their chance of predation and, consequently, expanding their occupation area in the water bodies.

The presence of natural fish cover and aquatic macrophytes were also important instream variables for predicting increased *P. reticulata* abundance. Natural cover structures are important components and regulators of freshwater ecosystems (Allouche 2002). Aquatic macrophytes, leaf banks, and living roots offer fish habitat refuge, with protection and isolation from predators and competitors (Allouche 2002; Smokorowski and Pratt 2007). In addition, these structures are important food items for freshwater fish and can also function as foraging sites, since they are a substrate for the growth of epiphytic algae and macroinvertebrates (Smokorowski and Pratt 2007). It should be noted that aquatic macrophytes are also associated with stream degradation, as they are favored by water nutrient enrichment and by the removal of riparian vegetation, which increases the availability of light (Barendregt and Bio 2003). Therefore, *P. reticulata*, an omnivorous and opportunistic species (Bueno et al. 2021; CABI 2021), may benefit from these conditions and resources from natural fish covers and, consequently, this can facilitate their establishment and increase their populations in recipient streams.

Stream habitat comprises all the biotic and abiotic variables that influence or provide sustenance to aquatic biota (Kaufmann et al. 1999). Our study investigated which physical habitat variables are most important for predicting the presence and abundance of the invasive fish *P. reticulata* in recipient streams. Guppy presence in the sampled streams was explained mainly by the human disturbance variables; however, the instream variables were important in predicting species abundance. Our results highlight the importance of urbanization in the invasion and establishment of *P. reticulata*. Urban areas are a relevant pathway for guppy introduction, and modifications in stream habitat caused by urbanization create distinct environmental conditions that benefit this invasive species. Identifying which habitat variables are favorable to the establishment of alien species is an important step toward controlling future biological invasions and managing those that have already occurred.

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References

Adelino JRP, Heringer G, Diagne C, Courchamp F, Faria LDB, Zenni RD (2021) The economic costs of biological invasions in Brazil: a first assessment. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) The economic costs of biological invasions around the world. NeoBiota 67: 349-374. https://doi.org/10.3897/neobiota.67.59185

Alexander ME, Kaiser H, Weyl OLF, Dick JTA (2015) Habitat simplification increases the impact of a freshwater invasive fish. Environ Biol Fish. 98: 477-486. doi:10.1007/s10641-014-0278-z

Allouche S (2002) Nature and functions of cover for riverine fish. Bull Fr Pêche Piscic. 365/366: 297-324. doi:10.1051/kmae:2002037

Angermeier PL, Wheeler AP, Rosenberger AE (2004) A Conceptual Framework for Assessing Impacts of Roads on Aquatic Biota, Fisheries, 29(12): 19-29

Barendregt A, Bio AM (2003) Relevant variables to predict macrophyte communities in running waters. Ecological modelling, 160 (3): 205-217

Base de Dados Nacional de Espécies Exóticas Invasoras (2021) Instituto Hórus de Desenvolvimento e Conservação Ambiental, Florianópolis – SC. http://bd.institutohorus.org.br. Accessed 05 October 2021

Breiman L (2001) Random forests. Machine Learning 45(1): 15-32. doi:10.1023/A:1010933404324

Borden JB, Flory SL (2021) Urban evolution of invasive species. Front Ecol Environ. doi:10.1002/fee.2295

Bueno ML, Magalhães ALB, Andrade Neto FR, Alves CBM, Rosa DM, Junqueira NT, Pessali TC, Pompeu PS, Zenni RD (2021) Alien fish fauna of southeastern Brazil: species status, introduction pathways, distribution and impacts. Biol Invasions. https://doi.org/10.1007/s10530-021-02564-x

CABI (2021) Invasive species compendium - Poecilia reticulata (guppy). https://www.cabi.org/isc/datasheet/68208. Accessed 04 August 2021

Callisto M, Alves CBM, Lopes JM, Castro MA (org.) (2014) Condições ecológicas em bacias hidrográficas de empreendimentos hidrelétricos. Belo Horizonte: Companhia Energética de Minas Gerais, v. 1, p. 47-68. (Série Peixe Vivo, 2)

Casatti L, Ferreira CP, Carvalho FR (2009) Grass-dominated stream sites exhibit low fish species diversity and dominance by guppies: an assessment of two tropical pasture River basins. Hydrobiologia 632: 273-283

Casatti L, Langeani F, Ferreira CP (2006) Effects of physical habitat degradation on the stream fish assemblage structure in a pasture region. Environ Manage. 38: 974-982. doi:10.1007/s00267-005-0212-4

Cruz LC, Pompeu PS (2020) Drivers of fish assemblage structures in a Neotropical urban watershed. Urban Ecosystems. doi:10.1007/s11252-020-00968-6

Cui L, Shi J (2012) Urbanization and its environmental effects in Shanghai, China. Urban Climate. 2: 1-15. doi:10.1016/j.uclim.2012.10.008

Cutler DR, Edwards Jr TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random forests for classification in Ecology. Ecology, 88: 2783-2792. https://doi.org/10.1890/07-0539.1

Dawson W, Moser D, van Kleunen M, Kreft H, Pergl J, Pyšek P, Weigelt P, Winter M, Lenzner B, Blackburn TM, Dyer EED, Cassey P, Scrivens SL, Economo EP, Guénard B, Capinha C, Seebens H, García-Díaz P, Nentwig W, García-Berthou E, Casal C, Mandrak NE, Fuller P, Meyer C, Essl F (2017) Global hotspots and correlates of alien species richness across taxonomic groups. Nat Ecol Evol 1:0186. https://doi.org/10.1038/s41559-017-0186

de Carvalho DR, Flecker AS, Alves CBM, Sparks J, Pompeu PS (2019) Trophic responses to aquatic pollution of native and exotic livebearer fishes. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2019.05.092

de Carvalho DR, Castro DMP, Callisto M, Moreira MZ, Pompeu PS (2017a) The trophic structure of fish communities from streams in the Brazilian Cerrado under different land uses: an approach using stable isotopes. Hydrobiologia. 795(1): 199-217. doi: 10.1007/s10750-017-3130-6

de Carvalho DR, Leal CG, Junqueira NT, Castro MA, Fagundes DC, Alves CBM, Hughes RM, Pompeu PS (2017b) A fish-based multimetric index for Brazilian savanna streams. Ecological Indicators, 77: 386–396. doi: 10.1016/j.ecolind.2017.02.032

Dias MS, Faria IF, Guarido PCP, Teresa FB, Aquino PDPU, Quimbayo JP (2020) Historical distribution and current drivers of guppy occurrence in Brazil. Journal of Fish Biology. doi:10.1111/jfb.14271

Dinno A (2018) paran: Horn's Test of Principal Components/Factors. R package version 1.5.2. https://CRAN.R-project.org/package=paran

Froese R, Pauly D (2021) FishBase. World Wide Web electronic publication. www.fishbase.org

Gallardo B (2014) Europe’s top 10 invasive species: relative importance of climatic, habitat and socio-economic factors. Ethology Ecology & Evolution, 26(2-3): 130-151. doi:10.1080/03949370.2014.896417

Ganassin MJM, Frota A, Muniz CM, Baumgartner MT, Hahn NS (2019) Urbanisation affects the diet and feeding selectivity of the invasive guppy *Poecilia reticulata*. Ecol Freshw Fish. 00:1-14. doi:10.1111/eff.12511

Garcia DAZ, Pelicice FM, Brito MFG, Orsi ML, Magalhães ALB (2021) Peixes não-nativos em riachos no Brasil: estado da arte, lacunas de conhecimento e perspectivas. Oecologia Australis. 25 (2): 565-587. https://doi.org/10.4257/oeco.2021.2502.21

Gherardi F (2007) Biological invasions in inland waters: an overview. In: Gherardi F (Ed.) Biological invaders in inland waters: Profiles, distribution, and threats. Invading Nature - Springer Series In Invasion Ecology, vol 2. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-6029-8_1

Gomes-Silva G, Cyubahiro E, Wronski T, Riesch R, Apio A, Plath M (2020) Water pollution affects fish community structure and alters evolutionary trajectories of invasive guppies (*Poecilia reticulata*). Science of The Total Environment, 138912. doi: 10.1016/j.scitotenv.2020.1389

Guimarães Silva R, Zenni RD, Rosse VP, Bastos LS, van den Berg E (2020) Landscape-level determinants of the spread and impact of invasive grasses in protected areas. Biol Invasions. 22: 3083-3099. doi:10.1007/s10530-020-02307-4

Hughes RM, Peck DV (2008) Acquiring data for large aquatic resource surveys: the art of compromise among science, logistics, and reality. J. N. Am. Benthol. Soc. 27: 837–859.

IPBES (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. Brondizio, J. Settele, S. Díaz, H. T. Ngo (Eds.). IPBES secretariat, Bonn, Germany, p. 1148. https://doi.org/10.5281/zenodo.3831673.

Jones Z, Linder F (2015) Exploratory data analysis using random forests. In: Proceedings of the 73rd Annual Mpsa Conference.

Junqueira NT (2011) Ictiofauna de riachos da bacia do rio Araguari, MG: estrutura, composição e relações com aspectos geográficos e amostrais. Dissertação de mestrado. Universidade Federal de Lavras.

Kassambara A, and Mundt F (2020) factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7. https://CRAN.R-project.org/package=factoextra

Kaufmann PR, Levine P, Robison EG, Seeliger C, Peck DV (1999) Quantifying Physical Habitat in Wadeable Streams. EPA/620/R-99/003. U.S. Environmental Protection Agency, Washington, D.C.

Le S, Josse J, Husson F (2008) FactoMineR: An R Package for Multivariate Analysis. Journal of Statistical Software, 25(1), 1-18. doi: 10.18637/jss.v025.i01

Leal CG, Pompeu PS, Gardner TA, Leitão RP, Hughes RM, Kaufmann PR, Zuanon J, de Paula FR, Ferraz SFB, Thomson JR, Nally RM, Ferreira J, Barlow J (2016) Multi-scale assessment of human-induced changes to Amazonian instream habitats. Landscape Ecology, 31(8): 1725–1745. doi: 10.1007/s10980-016-0358-x

Leão TCC, Almeida WR, Dechoum M, Ziller SR (2011) Espécies Exóticas Invasoras no Nordeste do Brasil: Contextualização, Manejo e Políticas Públicas. Recife: Cepan.

Leprieur F, Beauchard O, Blanchet S, Oberdorff T, Brosse S (2008) Fish invasions in the world's river systems: when natural processes are blurred by human activities. Plos Biology, 6: Pe322. doi: 10.1371/journal.pbio.0060028

Lewis SL, Maslin MA (2015) Defining the Anthropocene. Nature. 519: 171-180. doi:10.1038/nature14258

Liaw A, Wiener M (2002) Classification and Regression by randomForest. R News 2(3): 18-22

Macedo DR, Pompeu PS, Morais L, Castro MA, Alves CBM, França JS, Sanches B, Uchôa J,Callisto M (2014) Uso e ocupação do solo, sorteio de sítios amostrais, reconhecimento em campo e realização de amostragens. In: Callisto M, Alves CBM, Lopes JM, Castro MA (org.) Condições ecológicas em bacias hidrográficas de empreendimentos hidrelétricos. Belo Horizonte: Companhia Energética de Minas Gerais, v. 1, p. 47-68. (Série Peixe Vivo, 2)

Marques PS, Manna LR, Frauendorf TC, Zandonà E, Mazzoni R, El-Sabaawi R (2020) Urbanization can increase the invasive potential of alien species. J Anim Ecol, 89: 2345–2355. https://doi.org/10.1111/1365-2656.13293

Meffe GK, Snelson FF (1989) An ecological overview of Poeciliid fishes. In: Meffe GK and Snelson FF (eds.), Ecology and Evolution of Livebearing Fishes (Poeciliidae). Prentice Hall, Englewood Cliffs, NJ, pp. 13–31

Nentwig W (2008) Biological Invasions: why it Matters. In: Nentwig W. (eds) Biological Invasions. Ecological Studies (Analysis and Synthesis), vol 193. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-36920-2_1

Peck DV, Herlihy AT, Hill BH, Hughes RM, Kaufmann PR, Klemm DJ, Lazorchak JM, Mccormick FH, Peterson SA, Ringold PL, Magee T, Cappaert M (2006) Environmental monitoring and assessment program-surface water western pilot study: field operations manual for wadeble streams, U.S. Environmental Protection Agency, Office of Research and Development, Washington, DC.

Pelicice FM, Azevedo-Santos VM, Vitule JRS, Orsi ML, Lima-Junior DP, Magalhães ALB, Pompeu PS, Petrere-Junior M, Agostinho AA (2017) Neotropical freshwater fishes imperilled by unsustainable policies. Fish Fish 18(6): 1119-1133

Pelicice FM, Bialetzki A, Camelier P, Carvalho FR, García-Berthou E, Pompeu PS, Teixeira de Mello FT, Pavanelli CS (2021) Human impacts and the loss of Neotropical freshwater fish diversity. Neotrop Ichthyol. 19 (3): e210134. https://doi.org/10.1590/1982-0224-2021-0134

Peressin A, Casarim R, Prado IG, Cetra M (2020) Physical habitat as predictor of fish trophic structure in Brazilian Atlantic rainforest streams. Neotrop Ichthyol 18(2): e190076. https://doi.org/10.1590/1982-0224-2019-0076

Pinto BC, Araújo FG (2007) Assessing of biotic integrity of the fish community in a heavily impacted segment of a tropical river in Brazil. Braz. Arch. Biol. Technol. 50: 489-502

Pyšek P, Hulme PE, Simberloff D, et al. (2020) Scientists' warning on invasive alien species. Biol. Rev. 95, pp. 1511-1534. doi:10.1111/brv.12627

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reynolds SA, Aldridge DC (2021) Global impacts of invasive species on the tipping points of shallow lakes. Global Change Biology. 00: 1-10. https://doi.org/10.1111/gcb.15893

Ricciardi A, Blackburn TM, Carlton JT, et al. (2017) Invasion Science: A Horizon Scan of Emerging Challenges and Opportunities. Trends in Ecology & Evolution. 32(6): 464-474. doi:10.1016/j.tree.2017.03.007

Ricciardi A, MacIsaac HJ (2011) Impacts of Biological Invasions on Freshwater Ecosystems. In: Richardson DM (Ed.) Fifty Years of Invasion Ecology. https://doi.org/10.1002/9781444329988.ch16

Seebens H, Blackburn TM, Dyer EE, et al. (2017) No saturation in the accumulation of alien species in the worldwide. Nature Communications, 8 (14435). doi: 10.1038/ncomms14435

Seebens H, Blackburn TM, Dyer EE, et al. (2018) Global rise in emerging alien species results from increased accessibility of new source pools. Proceedings of the National Academy of Sciences, 115 (10): E2264–E2273. doi: 10.1073/pnas.1719429115

Smokorowski KE, Pratt TC (2007) Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – a review and meta-analysis. Environmental Reviews. 15 (NA): 15-41. doi:10.1139/a06-007

Strahler AN (1957) Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38, 913–920

Torremorell A, Hegoburu C, Brandimarte AL, et al. (2021) Current and future threats for ecological quality management of South American freshwater ecosystems. Inland Waters, 11(2): 125-140. doi: 10.1080/20442041.2019.1608115

Vilà M, Dunn AM, Essl F, Gómez-Díaz E, Hulme PE, Jeschke JM, Núñez MA, Ostfeld RS, Pauchard A, Ricciardi A, Gallardo B (2021) Viewing Emerging Human Infectious Epidemics through the Lens of Invasion Biology. BioScience 71(7): 722-740. https://doi.org/10.1093/biosci/biab047

Warbanski ML, Marques P, Frauendorf TC, Phillip DAT, El-Sabaawi RW (2017) Implications of guppy (*Poecilia reticulata*) life-history phenotype for mosquito control. Ecology and Evolution, 7(10): 3324-3334. doi:10.1002/ece3.2666

Wei T, Simko V (2021) R package 'corrplot': Visualization of a Correlation Matrix (Version 0.90). Available from https://github.com/taiyun/corrplot

Zandonadi L, Acquaotta F, Fratianni S, Zavattini JA (2016). Changes in precipitation extremes in Brazil (Paraná River Basin). Theor Appl Climatol, 123(3-4), 741–756. https://doi.org/10.1007/s00704-015-1391-4

CONSIDERAÇÕES FINAIS

Invasões biológicas e a degradação de habitat são grandes ameaças à biodiversidade nativa. Estes distúrbios provocados pelo homem estão aumentando rapidamente, sem nenhuma evidência de diminuição. Ecossistemas degradados, como áreas urbanas, podem ser pontos críticos para a entrada e o estabelecimento de espécies invasoras. O número de espécies exóticas de peixes introduzidas em bacias hidrográficas do Sudeste, área mais desenvolvida economicamente e densamente povoada do Brasil, vem crescendo ao longo do tempo. Listamos 201 espécies de peixes que estão introduzidas nesta região, sendo muitas delas invasoras nas bacias hidrográficas estudadas. Além da modificação das características físicas dos cursos d'água, com a diminuição da integridade biótica, isso pode ser atribuído ao volume de introduções feitas pelo homem, bem como pelo aumento do número de vias e facilidade de introdução. Estas mudanças na estrutura, dinâmica e funcionamento dos ecossistemas dulcícolas podem favorecer o estabelecimento e invasão de espécies, como no caso da espécie *Poecilia reticulata.* Identificamos que a presença deste peixe invasor nos riachos receptores foi explicada principalmente pelas variáveis de distúrbio humano relacionadas à urbanização, enquanto as variáveis de morfologia do canal e abrigo para peixes foram importantes para determinar se esta espécie será abundante nos locais onde foi introduzida.

Estratégias para prevenção de futuras introduções de espécies de peixes devem ser tomadas, pois, uma vez estabelecidas, é quase impossível erradicá-las. Além disso, há uma necessidade de esforços mais eficazes na coleta de dados e classificação dos impactos que estas espécies invasoras de peixes causam nos ecossistemas receptores. O método EICAT (Environmental Impact Classification for Alien Taxa, IUCN), por exemplo, é uma importante ferramenta para obter uma melhor compreensão da magnitude destes impactos e para alertar as partes interessadas para as possíveis consequências da introdução de espécies exóticas. Assim, o conhecimento gerado por esses estudos é muito importante para uma melhor comunicação entre comunidade científica, gestores e população, possibilitando a implementação de programas de gestão eficazes.