UNIVERSIDADE FEDERAL DO PARÁ
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
EMBRAPA AMAZÔNIA ORIENTAL
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

LUCAS FERREIRA COLARES

O papel da raridade e da sensibilidade à perda de habitat nos padrões de extinção funcional de peixes em riachos Amazônicos

Belém
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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Mestre em Ecologia.
Área de concentração: Ecologia.
Linha de Pesquisa: Ecologia de Comunidades e Ecossistemas

Orientadora: Profa. Dra. Bárbara Dunck Oliveira
Coorientador: Prof. Dr. Luciano Fogaça de Assis Montag

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Aprovada em: 27 de fevereiro de 2021
Local de defesa: vídeo conferência, através da plataforma Google Meet.

Dados Internacionais de Catalogação na Publicação (CIP) de acordo com ISBD
Sistema de Bibliotecas da Universidade Federal do Pará
Gerada automaticamente pelo módulo Ficat, mediante os dados fornecidos pelo(a) autor(a)

C683p Colares, Lucas Ferreira.
O papel da raridade e da sensibilidade à perda de habitat nos padrões de extinção funcional de peixes em riachos Amazônicos / Lucas Ferreira Colares. — 2021.
95 f. : il. color.

Orientador(a): Profª. Dra. Bárbara Dunck
Coorientador(a): Prof. Dr. Luciano Fogaça de Assis Montag
Dissertação (Mestrado) - Universidade Federal do Pará, Instituto de Ciências Biológicas, Programa de Pós-Graduação em Ecologia, Belém, 2021.

1. Traços funcionais. 2. Raridade funcional. 3. Uso de solo. 4. Desmatamento. 5. Ecologia trófica. I. Título.

CDD 574.522209811

DEDICATÓRIA

My mom always told me that I
would make it,

So, I made it.

AGRADECIMENTOS

Primeiramente, sou extremamente grato aos meus orientadores, Bárbara Dunck e Luciano Montag, pela jornada incrível nos últimos anos. Vocês não têm ideia do quanto contribuíram para o meu desenvolvimento profissional. Vocês dois são minha inesgotável fonte de inspiração na academia.

Agradeço imensamente aos meus amigos e família pelo suporte em momentos difíceis e por sempre acreditarem no meu potencial. Nada do que foi desenvolvido em minha carreira cientifica até agora seria possível sem o apoio de vocês, portanto, obrigado.

Obrigado aos meus professores durante o mestrado. Mesmo quando eu achei que não iria aprender nada novo em uma disciplina, vocês me provaram errado. O conhecimento que adquiri com vocês não tem preço e, mesmo se tivesse, eu não venderia por nada nesse mundo. Obrigado também ao Programa de Pós-Graduação em Ecologia da Universidade federal do Pará por ter me acolhido tão bem durante o mestrado.

Especificamente, gostaria de agradecer aos professores Helder Mateus Viana Espírito-Santo, Karl Cottenie, Rafael Leitão, Fernando Rodrigues da Silva, Fabrício Barreto Teresa e Roger Paulo Mormul pelos seus comentários valiosos em versões anteriores desta dissertação.

Agradeço à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa concedida a mim durante o mestrado. Agradeço também à CIKEL Ltda., 33 Forest Capital, Instituto Floresta Tropical, e Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) pelo apoio financeiro e logístico concedido para a realização deste trabalho.

O papel da raridade e da sensibilidade à perda de habitat nos padrões de extinção funcional de peixes em riachos Amazônicos

RESUMO

A perda de habitat é uma das principais ameaças à biodiversidade no Antropoceno, frequentemente culminando na extinção de espécies e mudanças no funcionamento do ecossistema. Quando uma espécie é extinta, o papel que ela desempenhava na manutenção do ecossistema e da comunidade também é extinto, se nenhuma outra espécie desempenhar o mesmo papel. O risco de extinção depende da abundância, distribuição geográfica e sensibilidade ambiental das espécies, e dessa forma, espécies raras em relação a estes três aspectos estão em maior risco de extinção. Além disso, o risco de perda funcional também depende da raridade funcional das espécies, no qual traços funcionais distintos fornecidos por poucas espécies devem estar mais vulneráveis à extinção do que traços suportados por muitas espécies. Para investigar o papel da raridade e da perda de habitat nos padrões de extinção funcional de peixes em riachos Amazônicos, nós desenvolvemos dois estudos, os quais os principais objetivos foram (1) investigar o papel da raridade das espécies na perda de traços funcionais e na raridade funcional das comunidades; e (2) investigar o papel da perda de habitat na perda de traços funcionais e na raridade funcional da comunidade. Para o primeiro estudo, amostramos a comunidade de peixes de 40 riachos pristinos na bacia do rio Capim, Amazônia oriental. Já pro segundo estudo, nós expandimos nossa amostragem para 63 riachos, na mesma bacia, que diferiam em relação ao uso e ocupação da terra, incluindo os 40 riachos pristinos do primeiro estudo. Para os dois estudos, nós atribuímos um traço funcional baseado na proporção de dieta de cada espécie, divido em sete categorias funcionais. Para o primeiro estudo, calculamos a raridade das espécies baseada na abundância local e ocorrência regional das espécies. Desenvolvemos cenários de extinção onde as espécies foram extintas das mais raras para as mais comuns (e vice-versa) e comparamos com cenários aleatórios de extinção. Para o segundo estudo, nós calculamos a integridade de habitat baseada em sete variáveis ambientais mensuradas nos riachos e determinamos a sensibilidade ambiental das espécies através de uma análise de limiares de táxons indicadores (*Threshold Indicator Taxa Analysis*; TITAN). Determinamos a sensibilidade ambiental das espécies como o mínimo de integridade necessária para que a espécie sobreviva, como retornado pelo TITAN. Posteriormente, nós construímos um modelo aditivo que considerou a raridade das espécies (como abundância e ocorrência) somado à sua sensibilidade ambiental. Dessa forma, nós consideramos espécies raras que só sobrevivem em habitats íntegros como sensíveis, e espécies comuns que conseguem sobreviver em baixa integridade de habitat como tolerantes. Finalmente, desenvolvemos cenários de extinção onde as espécies de peixes foram extintas das mais sensíveis para as mais tolerantes (e vice-versa) e comparamos com cenários aleatórios de extinção. No primeiro estudo, as espécies raras são as mais distintas funcionalmente nas duas escalas. Já no segundo estudo, espécies sensíveis são as mais distintas funcionalmente em escala local, mas em escala regional as espécies tolerantes são mais únicas funcionalmente. Independente da escala, quando espécies raras ou sensíveis são extintas primeiro, o ecossistema sofre uma perda funcional brusca após um limiar de até 15% de espécies extintas, em contraste com espécies comuns e tolerantes, que suportaram a extinção de >80% de espécies até a perda da primeira função. Se espécies raras e sensíveis forem realmente as primeiras a serem extintas após a perda de habitat, então podemos esperar que o ecossistema de riacho amazônico colapse graças à extinção de peixes detritívoros, piscívoros, algívoros e hematófagos, as categorias funcionais com maior risco de extinção nos dois estudos.

Palavras-chave: Traços funcionais efeito. Ecologia trófica. Água doce. Extinção em massa. Ecossistema tropical. Desmatamento. Uso da terra.

The role of rarity and vulnerability to habitat loss in functional extinction patterns of fish from Amazon streams

ABSTRACT

Habitat loss is the major threat to biodiversity in the Anthropocene, often leading to species extinction and further changes in ecosystem and community dynamics. Once species are extinct, the role that once it played in the ecosystem and community maintenance also disappear if no other species continue to provide the same role in the ecosystem. The risk of extinction depends on species' abundance, geographical distribution, and habitat breadth, with rare species regarding each of these three aspects being at higher risk of extinction. The risk of functional extinction also depends on the functional rarity of species, with distinct traits provided by few species being more vulnerable to functional extinction than redundant ones. To disentangle the role of rarity and habitat loss in functional extinction of fish from Amazon streams, we developed two studies which main goals were (1) to investigate and scale the role of rarity in the loss of functional traits and functional rarity from fish communities; (2) and to investigate the role of habitat loss in the loss of functional traits and rarity from fish communities. For the first study, we sampled the fish community of 40 pristine streams in Capim river basin, eastern Amazon. For the second study, we expanded our samples to 63 streams in different land-uses from the Capim river basin, including the 40 streams from the first study. We assigned one functional trait based in the proportion of diet of each species, divided into seven functional categories. For the first study, we calculated species' rarity based on their abundance, at local scale, and occurrence, at regional scale. We built extinction scenario that extinguished species from the rarest to the commonest (and vice versa) and compared to random scenarios of extinction. For the second study, we calculated the habitat integrity based on seven environmental variables measured in each stream and determined species' habitat breadth using Threshold Indicator Taxa Analysis (TITAN). We determined species' vulnerability to habitat loss as the minimum of integrity required by species to occur in streams. We built an additive model in the second study that considered species' rarity (as abundance and occurrence) and its vulnerability to habitat loss, in this way, we considered as sensible species to habitat loss species with low abundance or occurrence and which survive only under high habitat integrity, and tolerant species as the ones with high abundance or occurrence and which are able to persist under low habitat integrity. We built extinction scenario that extinguished species from the most sensible to the most tolerant (and vice-versa) and compared to random scenarios of extinction. In the first study, we found that rare species, at local and regional scale, are more functionally distinct than common species. As for the second study, we found that sensible species are the distinct ones at local scale, but at the regional scale, tolerant species are the ones supporting unique functional traits, what may assure the resilience of the region. Regardless of the scale, when rare, in the first study, and sensible species, in the second study, were extinct, an abrupt loss of functions happened with the extinction of up to 15% of the species, in contrast with common and tolerant species, which supported the extinction of more than 80% of species until the first loss of function. If habitat loss indeed targets rare and sensible species to extinction, we can expect that Amazon streams collapse through the loss of detritivore, piscivore, algivore and hematophagous fish, the functional categories frequently at higher risk of extinction in both studies.

Key-words: Functional effect traits. Trophic ecology. Freshwater. Mass extinction. Tropical ecosystem. Deforestation. Land-use.

SUMÁRIO

INTRODUÇÃO GERAL

Durante os últimos séculos, os seres humanos vêm destruindo e degradando habitats naturais, introduzindo espécies exóticas, alterando o clima do planeta e seletivamente dizimando espécies (DIRZO *et al.*, 2014). Estas e outras atividades humanas desencadearam um sexto evento de extinção em massa na história do planeta, onde espécies estão sendo extintas mil vezes mais rápido do que o esperado naturalmente (PIMM *et al.*, 2014). Tendo em vista a rápida extinção de espécies no Antropoceno, cientistas têm investigado quais fatores contribuem para a vulnerabilidade à extinção das espécies afim de identificar quais espécies estão mais em risco de extinção (PIMM *et al.*, 2014).

A raridade tem sido constantemente indicada como um fator determinante no risco de extinção das espécies (HULL; DARROCH; ERWIN, 2015; VIOLLE *et al.*, 2017) e pode ser expressa em três principais formas: abundância local; distribuição geográfica; e sensibilidade à distúrbios (HARNIK; SIMPSON; PAYNE, 2012; RABINOWITZ, 1981). Em termos de abundância, a população de uma espécie pode ser composta por poucos ou muitos indivíduos, sendo que populações de poucos indivíduos estão mais vulneráveis à extinção, tendo em vista que poucos indivíduos precisam ser perdidos até que a espécie seja extinta (VIOLLE *et al.*, 2017). Em relação à distribuição geográfica, espécies podem ser amplamente distribuídas em diferentes populações em uma região ou restritas, distribuídas em poucas populações em uma região endêmica (LEITÃO *et al.*, 2016). Dessa forma, espécies com uma distribuição geográfica restrita estão mais vulneráveis à extinção, já que poucas populações precisam ser extintas até que a espécie desapareça da região (VIOLLE *et al.*, 2017). Já em relação à sensibilidade ambiental, algumas espécies persistem apenas em habitats íntegros específicos, e estas são espécies sensíveis à modificação de habitat. Em contraste, outras espécies persistem em diferentes habitats com diferentes condições ambientais, e estas são espécies tolerantes à modificação do habitat. Tendo em vista que o atual evento de extinção em massa está ocorrendo graças à grande modificação humana de habitats íntegros, espécies sensíveis estão em maior risco de extinção (BUENO *et al.*, 2018).

Quando uma espécie é extinta, não só a sua presença é perdida em determinado habitat, mas também o papel que aquela espécie antes desempenhava na dinâmica da comunidade e no funcionamento do ecossistema, especialmente se nenhuma outra espécie continuar desempenhando o mesmo papel no habitat (VIOLLE *et al.*, 2017). Uma das formas de se avaliar os papéis desempenhados por cada espécie no ecossistema é através da avaliação de traços funcionais efeito, que são características morfofisiológicas e/ou comportamentais mensuradas à nível de individuo ou espécie que refletem o efeito da espécie na comunidade e ecossistema onde vive (MAMMOLA *et al.*, 2020). Apesar da influência da abundância, distribuição geográfica e sensibilidade ambiental no risco de extinção das espécies, a raridade funcional também tem um papel fundamental determinando o risco de extinção funcional (perda de traços funcionais) em comunidades biológicas (LEITÃO *et al.*, 2016; SIQUEIRA *et al.*, 2012; VIOLLE *et al.*, 2017). Funcionalmente, as espécies podem desempenhar funções distintas ou redundantes em relação às outras que estão no mesmo local ou região, sendo consideradas distintas aquelas funções desempenhadas por uma única ou poucas espécies, em contrapartida com as funções redundantes, que são desempenhadas por muitas espécies ao mesmo tempo (BIGGS *et al.*, 2020). Portanto, funções distintas são mais vulneráveis à extinção, tendo em vista que é necessário a extinção de apenas uma ou poucas espécies até que a função seja extinta.

Diante do exposto, o objetivo desta dissertação foi investigar o papel das três principais formas de raridade nos padrões de extinção funcional de peixes em riachos Amazônicos. Especificamente, no Capítulo 1, investigamos o papel da abundância, em escala local, e distribuição geográfica, em escala regional, nos padrões de perda de raridade funcional e extinção de traços funcionais de peixes de riachos amazônicos. Já no Capítulo 2, construímos uma abordagem aditiva que combina a abundância, e distribuição geográfica, com a sensibilidade ambiental das espécies para, dessa forma, identificarmos o papel da modificação de habitat nos padrões de perda de raridade funcional e extinção de traços funcionais de peixes de riachos amazônicos.

Extinction of scarce and restrict fish species lead to abrupt functional losses in Amazonian streams

Formatado conforme as normas da publicação científica *Freshwater Biology*, disponível em: https://onlinelibrary.wiley.com/page/journal/13652427/homepage/forauthors.html

Extinction of scarce and restrict fish species lead to abrupt functional losses in Amazonian streams

Abstract

1. Species are being extinct faster than expected due to increasing human modification of natural habitat. When the extinction of a species culminates in the extinction of its role in ecosystem functioning, cascade effects occur throughout the community, altering ecosystem dynamics. The risk of functional extinction depends mainly on taxonomic and functional rarity, with non-redundant traits supported by rare species being more vulnerable.
2. To elucidate and scale the relationship between rarity and functional extinction, we developed simulations of extinction driven by species' rarity. First, we sampled the fish community of 40 pristine Amazon streams. Then, we assigned functional traits for each species related to its diet. Finally, we extinguished species from the rarest to the commonest (and vice-versa) and compared to random scenarios at a local and regional scale.
3. When the rarest species were extinct first, the community's functional rarity decreased, and the first functional category was lost after up to 15% of species extinct at local and regional scales. Otherwise, when the commonest were extinct first, the functional rarity increased, and the first functional category was lost after more than 85% of species extinct at both scales.
4. We observed that the extinction of rare and restrict species will bring detrimental effects to ecosystem functioning. If the ongoing mass extinction indeed targets rare species, we can expect Amazon streams to collapse due to the loss of detritivore, piscivore, algivore and hematophagous fish, the most vulnerable functional categories.

Introduction

Regardless of many definitions (Delord, 2007), it is widely accepted that extinction happens when the last individual of a species disappears from its geographical distribution (IUCN, 1994). It is a natural process that can occur at small scales, such as local extinction – when a species vanishes from a habitat but occurs in others (Leitão *et al.*, 2016) – and on large scales, such as global extinction – when a species vanishes from all its habitats on Earth (Hull, Darroch & Erwin, 2015). In the last centuries, humans have destroyed, fragmented and degraded natural habitats, introduced alien species, proliferated diseases, selectively killed species, and altered global climate with the development of human society (Barnosky *et al.*, 2011; Burkhead, 2012; Dirzo *et al.*, 2014; Pimm *et al.*, 2014). The unsustainable human population growth has triggered the sixth mass extinction event on Earth, where species are going extinct a thousand times faster than expected (Pimm *et al.*, 2014).

When a species goes extinct, the role that once it played in the dynamics of the community and ecosystem functioning is also gone if no other species continues to support the same role in the ecosystem (Violle *et al.*, 2017). Functional losses related to ecosystem and community maintenance can bring cascade effects to the environment, such as disruption of nutrient cycling (Taylor, Flecker & Hall, 2006). Moreover, functional extinction can bring changes in ecosystem processes, such as disruption of seed-dispersal (Pires *et al.*, 2018), pollination supported by insects (Crespo-Pérez *et al.*, 2020), decreases in nutrient release by fish and macro-invertebrates (Atkinson *et al.*, 2019), and shifts in species composition (Rees, Kingsford & Letnic, 2019).

The magnitude of impact from a functional extinction to the community or ecosystem depends on functional and taxonomical forms of rarity (Violle *et al.*, 2017). Rarity of the species has been pointed out as a determinant of species' extinction risk in past mass extinctions and current extinction events (Heim & Peters, 2011; Hull *et al.*, 2015), and can be expressed in several forms, such as geographical range or local abundance of species (Harnik, Simpson & Payne, 2012). Functionally, species can provide unique or redundant morpho-physiological and behavioural characteristics (i.e., functional traits) compared to others in the community that will influence community and ecosystem dynamics (Cadotte, Carscadden & Mirotchnick, 2011; Violle *et al.*, 2017). While few species provide unique functional traits, redundant traits are provided by many species. In this way, unique traits should be more vulnerable to extinction, given that it takes one or a few species to be extinct for a functional extinction to occur (Naeem, 1998; Violle *et al.*, 2017). Taxonomically, species can be abundant or rare in the habitat and widespread or restricted in their geographical range compared to other species. In this way, unique traits provided by rare/restricted species should be more vulnerable to extinction since fewer individuals/populations need to go extinct before the trait is lost (Mouillot *et al.*, 2013; Walker, 2016; Violle *et al.*, 2017). Nevertheless, ecologists are far from a consensus on the real impact of rare and restrict species on ecosystem functioning compared to abundant and widespread ones (Grime, 1998; Violle *et al.*, 2017; Dee *et al.*, 2019).

Some studies have focused on the relationship between taxonomic rarity and functional extinction (Mouillot *et al.*, 2013; Leitão *et al.*, 2016), mainly through indexes such as functional diversity and functional vulnerability. However, few studies scale and disentangle which traits are more vulnerable to extinction, its relationship with taxonomic rarity, and possible effects on ecosystem functioning after its extinction (Violle *et al.*, 2017). Specifically, the scaling of functional extinction patterns should reveal even more complex relationships between functional extinction and ecosystem functioning since species can change in functional and taxonomic rarity from one scale to another. A species may support a locally distinct functional trait compared to other species of the same stream. However, the same species may share its functional traits with other species from other streams within the region, assuring the functional resilience of the region (Violle *et al.*, 2017). The same is true to species' taxonomic rarity since a species can have a high local abundance compared to the others of the same stream but can occur only in few streams regionally (Violle *et al.*, 2017). For instance, a species may become an “ecological ghost” within a region when it is restricted to few sites, even if it is abundant in these sites, since it does not contribute significantly to ecosystem functioning in the region in comparison to widespread species (Hull *et al.*, 2015).

In this view, identifying the species which hold the most vulnerable functional traits considering different scales within a region may be useful in conservatory initiatives by giving direction to which species need urgent conservation to maintain ecosystem functioning and what may happen if they were extinct. Thus, identify species holding the most vulnerable traits should be especially urgent in highly diverse and threatened tropical ecosystems, such as Amazon. Data regarding biodiversity and its extinction risk is deficient in Amazon (Collen *et al.*, 2008; Hubbell *et al.*, 2009; Gueńard, Weiser & Dunn, 2012), and the forest support critical ecosystems processes that are currently threatened by human modification (Malhi *et al.*, 2008). Indeed, deforestation has been increasing in Amazon since 2012, reaching the highest peak of the past ten years in 2020 (TerraBrasilis, 2020). Land-use conversion, especially cattle ranching and soybean, has been the primary driver of this deforestation, and if current trends continue, we should expect 40% of forest loss by 2050 in Amazon (Soares-Filho *et al.*, 2006). Even with the current implementation of protected areas at Amazon, some essential ecosystems are still not entirely comprised within these areas, such as freshwater networks (Azevedo-Santos *et al.*, 2019), which, in Amazon, are responsible for about 20% of the world's freshwater discharge (Davidson *et al.*, 2012).

These freshwater ecosystems hold species networks with dependencies on energy exchanges with terrestrial habitats that have been ceaselessly exploited (Ballinger & Lake, 2006). Stream fish are an essential group to maintain stream functioning since they regulate energy exchanges with terrestrial habitats and within the stream through their relationships with other species (Zuanon & Ferreira, 2008). Thus, approaching the trophic networks to which fish participate in the stream can give insights about the effects that species may have in the ecosystem and community they live in (Flecker, 1996; Ballinger & Lake, 2006; Gelwick & Mcintyre, 2017). Stream fish are among the most vulnerable groups to extinction due to the recent human exploitation and are underrated in the conservation initiatives currently implemented in Amazon (Frederico, Zuanon & De Marco, 2018).

In this context, we attempted to elucidate and scale the relationship between taxonomic rarity and functional extinction, disentangling functional extinction's possible effects on stream ecosystem dynamics. To do so, we generated two different scenarios of species extinction driven by taxonomic rarity at local (in individual streams) and regional (in an entire basin) scales. We investigated three questions: (1) How the functional rarity of the community change as species goes extinct based on their taxonomic rarity at local and regional scales? (2) How the loss of functional traits changes as species goes extinct based on their taxonomic rarity at local and regional scales? (3) Which are the traits most likely to go extinct first in different extinction scenarios at local and regional scales? For the first question, we hypothesized that when rare/restrict species are extinct first, the functional rarity of the community will decrease, at either scale. Concerning the second question, functional losses would start after a few rare/restrict species being extinct, in contrast, many abundant/widespread species should be extinct for the first functional loss to occur. Rare and restrict species usually hold specialized traits not provided by others (Mouillot *et al.*, 2013; Leitão *et al.*, 2016), which means that if these species are extinct first, the community would rapidly lose unique traits, becoming less functionally distinct. On the other hand, when widespread/abundant species are extinct first, the pattern should be inverted since they hold functional traits usually redundant to other species (Leitão *et al.*, 2016; Violle *et al.*, 2017).

Methods

Field sampling

The fish sampling was conducted in 40 rainforest streams from first to third order in the Capim River basin, eastern Amazon, from 2012 to 2015 (Figure 1). The region is characterized by a dense ombrophilous forest with a warm-humid tropical clime and one rainy period from December to May and a dry period from June to November (Albuquerque *et al.*, 2010). The average annual temperature reaches 26°C and an annual rainfall of 2,344 mm^3, with a maximum of 427 mm^3 in May and a minimum of 54 mm^3 in September (Albuquerque *et al.*, 2010). The region is historically influenced by intense deforestation due to land use conversion, but some areas still comprise pristine rainforests within their area, where the streams were sampled (Figure 1). The sampled streams are characterized by low thalweg depth, high variation in incision height, a heterogeneous substrate (composed mainly of particles of <16 mm, such as sand, silt, mud, clay, and organic matter), and a large number of microhabitats, represented by wood fragments, roots, undercut banks and coarse litter (Benone *et al.*, 2017). The streams were collected in the dry period when discharge is low and sampling efficiency is high, and also to avoid seasonal variation among samples (Prudente *et al.*, 2017). We never sampled the same stream twice or more, and all streams were selected based on their accessibility. A minimum fluvial distance of 2 km between samples was used to avoid pseudoreplication. To ensure that our data was not spatially autocorrelated, we conducted a Moran's I to test if functional and taxonomic rarity were spatially structured (Moran, 1950). We concluded that there was no spatial autocorrelation among the sampled streams regarding their species composition, functional rarity, and taxonomic rarity, so we maintained all sampled sites in the following analysis (see Appendix S1).

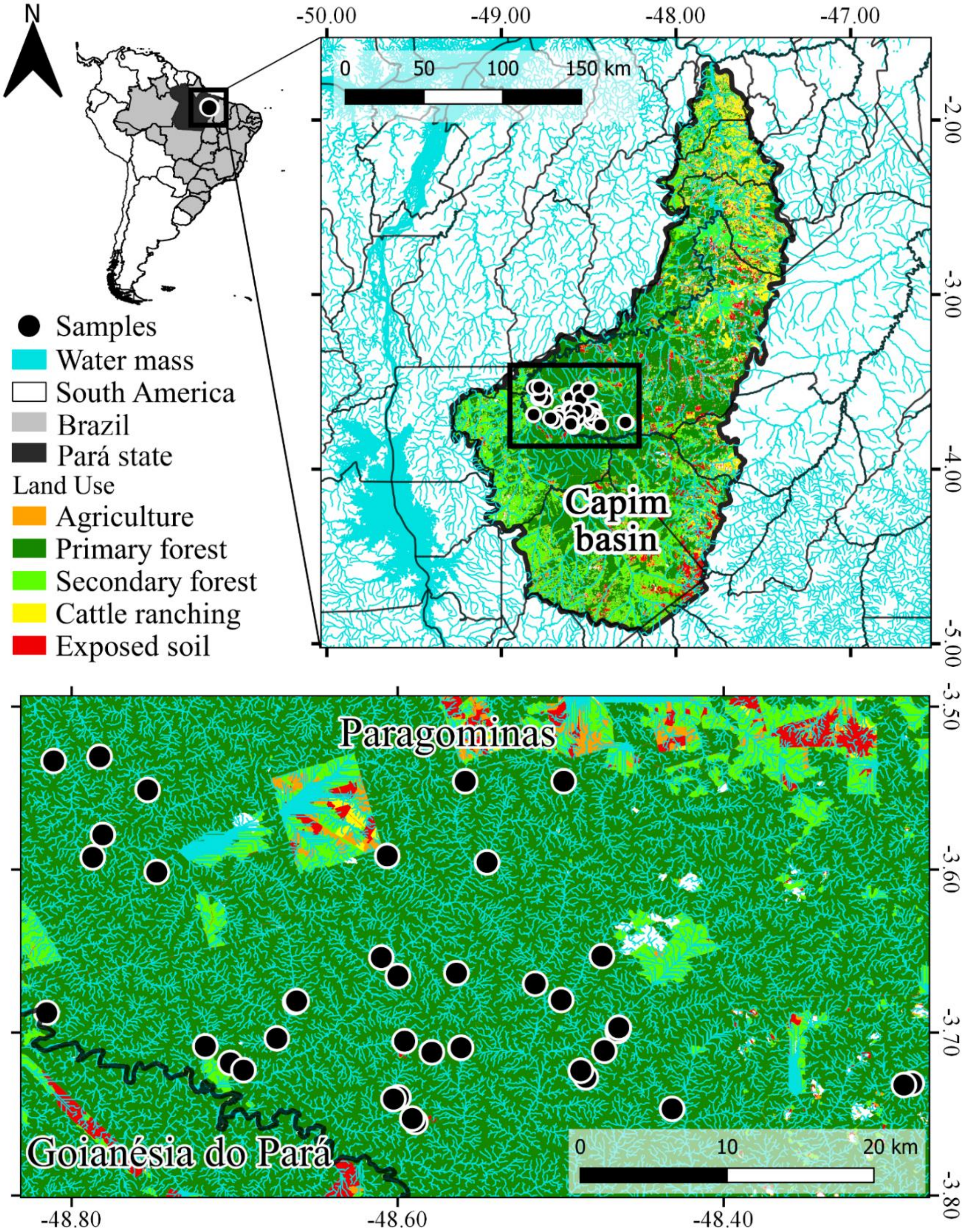

Figure 1. Geographical location of the 40 sampled streams and land use characterization in Capim river basin, eastern Amazon.

The fish were collected through active search using two circular 55-cm-diameter dip nets with 2-mm mesh in a 150 m stretch of each stream subdivided in 10 subsections (Montag *et al.*, 2019). Each subsection of the stream was sampled during 18 min, totalling a sampling efforts of three hours per stream. This method assures the sampling of the majority of microhabitats where fish live in streams, and it is a useful method considering the high heterogeneity of Amazonian stream habitat (Uieda & Castro, 1999). The fish sampled were euthanized through lethal doses of Eugenol anaesthetic and then fixed in formalin at 10% concentration for 72 hours. After, the fish were finally conserved in alcohol at 70% concentration for further taxonomic identification to the lowest taxonomic level possible using fish taxonomic literature (Albert, 2001; Reis, Kullander & Ferraris, 2003; Van der Sleen & Albert, 2018). The collecting method was approved by the Animal Ethics Committee (CEUA) under protocol number 8293020418 (UFPA).

Functional characterization

We assigned one functional trait related to the diet of the fish based on gut content and literature search. We choose this functional trait since it informs the relationships between species and the ecosystem processes that they maintain. The diet functional trait was selected due to its capacity to predict the *effects* of functional extinction in ecosystem functioning instead of identifying the community's response to environmental changes (Violle *et al.*, 2007). The possible effects of the extinction of each functional category to the ecosystem and community dynamics are described in Appendix S1 – Table B1. The trait was divided into seven functional categories: (1) Autochthonous invertivore (feed on adult forms of aquatic invertebrates); (2) allochthonous invertivore (feed on adult forms of terrestrial invertebrates); (3) piscivore (feed on other fish); (4) algivore (feed on algae); (5) larvivorous (feed on the larvae state of aquatic and some terrestrial organisms); (6) detritivore (feed on the organic matter in the bottom of stream); and (7) hematophagous (feed on blood). The extinction of categories of diet can bring cascade effects to other species and the ecosystem (Table 1).

Table 1. Diet functional trait, its respective categories (functions), and why they are important in ecosystem functioning and community dynamics. Information from the "Why is this function important?" and its references support the post-extinction scenario of functions in Fig. 5.

Functional effect trait	**Categories**	**Why is this function important?**
DIET	Autochthonous invertivore	These are fish who feed on adult aquatic invertebrates. When autochthonous invertivore fish are present in the stream, they control the population of grazing invertebrates, thus lowering the predation pressure on periphytic algae (Hargrave *et al.*, 2006). This top-down control allows higher algae biomass and higher primary production in the ecosystem (Hargrave, 2006). Beyond, Hargrave *et al.* (2006) indicates that when autochthonous invertivore fish decreases the density of grazing invertebrates, it leads to lower competition among grazer species, allowing for higher growth of grazer fish.
	Allochthonous invertivore	These are fish who feed on adult terrestrial invertebrates. They actively translocate nutrients between terrestrial and aquatic ecosystems, providing "new" nutrients in the stream (Vanni, 2002). This enhanced nutrient input allows for higher primary productivity, thus more complex trophic interactions and higher densities of consumers (Hargrave, 2006). In this view, ecosystems where this function is played by fish usually present higher primary and secondary productivity (Nakano & Murakami, 2001).
	Piscivore	These fish directly control the population of its prey. Experimental studies have previously related cascade trophic effects of these predatory fish on invertivores fish biomass and growth (Gilliam, Fraser & Alkins-Koo, 1993; Greenberg, Dahl & Bergman, 2005; Lovell *et al.*, 2017). Gilliam *et al.* (1993) evidenced that the presence of the piscivore *Hoplias malabaricus* led to lower biomass of a preyed invertivorous fish in tropical streams, which only presented small individuals in sites where the predator was present.
	Algivore	These are fish who feed on phytoplankton or periphytic algae. They control the algae population in streams, allowing the coexistence between species and higher diversity of algae (Power, Stewart & Matthews, 1988; Flecker, 1996). When algivore fish are present, the biomass of diatoms tends to decrease while the biomass of nitrogen-fixing cyanobacteria increases, as these cyanobacteria are facilitated by algivores (Power *et al.*, 1988; Flecker, 1996). The extinction of this functional category can trigger a eutrophication process in the stream if environmental conditions are already degraded, creating a hypoxic system with low visibility and water quality due to algae overgrowth (Flecker et al., 2002).

Detritivore	These are fish who explore the organic matter accumulated in the stream bottom. They assure the nutrient cycling in the ecosystem, releasing the organic carbon locked in the organic matter in the ecosystem to be used by other organisms in the trophic web (Flecker, 1996; Taylor *et al.*, 2006). Beyond interfering in its stream, detritivore species also ensure the release of organic carbon downstream, as the nutrient is carried by streamflow (Taylor *et al.*, 2006).
Larvivorous	These fish control the population of its larvae prey, influencing the adult population densities of these organisms (Wesner, 2010). Experimental studies have shown that the effects that larvivorous fish may have in the community cross boundaries of ecosystems, for example, fish who feed on Dragonfly and Mosquito aquatic larvae decreases the population of the insects in the adult phase, at the terrestrial habitat (Chandra *et al.*, 2008; Wesner, 2010). Larvivorous fish are effectively at controlling the biomass of Mosquitos that are vectors of human diseases, such as malaria and dengue fever, common diseases in the tropics (Chandra *et al.*, 2008; De Góes Cavalcanti *et al.*, 2009).
Hematophagous	These fish feed on the blood of other fish, making an incision on the gills arteries and engorging themselves in the blood (Zuanon & Sazima, 2004). They can kill its host (although it is rare) but mainly makes its host more vulnerable to diseases and infections due to the open incision they left in the host's blood system (Spotte, 2002; Zuanon & Sazima, 2004). As hematophagous weakens its host and indirectly leads to its death is an important function itself, as it contributes to nutrient cycling by leaving its host body to be decomposed. Beyond, the death of the host reduces intraspecific competition among its host in the stream, allowing the coexistence of multiple species. The species in our study (*Paracanthopoma* sp.) uses its host to migrate between water bodies, in this way, this hematophagous contributes to the input of "new" translocate nutrients between streams and rivers trough excretion (Zuanon & Sazima, 2005).

We analysed the ichthyofauna's digestive tract to assign the diet functional trait to species. First, six individuals of each species were selected haphazardly, except for species with fewer individuals, with similar body sizes, to avoid ontogenetic influence on the species' diet. Food items were identified to the lowest taxonomic level possible, under an optical microscope, using specialized literature (Mugnai, Nessimian & Baptista, 2010; Hamada, Nessimian & Querino, 2014) and with the help of specialists from different taxonomic groups. The percentage of dominance that each food item occupied in each individual's digestive tract's total volume was quantified by visual estimate (Hyslop, 1980). To accurately assign diet, we combined digestive tract analysis with diet information previously published in the literature for the sampled species (see Appendix S1 for a detailed list of the studies we used to assign the diet functional trait). When studies used an alimentary index to inform species diet, we corrected the index scale to a scale ranging from 0 to 100. We then summed the index with the percentage of the dominance of food items found in the species' digestive tract. Otherwise, when studies categorized the species' diet, we summed a value of 100 for each diet category cited for the species. We did not take into account studies that classified species only as omnivorous, with no further details. After, we transformed our diet data into a fuzzy-type matrix that measures the proportions of each diet category to each species (Pavoine *et al.*, 2009). The diet trait is a fuzzy-type trait, so we are not categorizing species into each functional category but instead assigning values of proportions of each category to each species. This way, a single species can contribute in different strengths to two or more functional categories. This plasticity in the diet of some stream fish can give insights about the role of redundancy in the stability of stream ecosystem (Sanders *et al.*, 2018).

Species' rarity

We determined taxonomic and functional rarity at two different scales: (1) local, considering each community in each stream; and (2) regional, considering all the species in the whole basin (all streams. To measure taxonomic rarity, we used a local scarcity index (*Sc*), which is basically the inverse of species' relative abundance, but it ranges from 0 to 1 and has a pivotal value of 0.5 for species with a relative abundance corresponding to $1/N$, as N is the number of species in the community (Violle *et al.*, 2017). When the relative abundance of species i (Ab_i) is higher than its expectation under a perfect evenly distribution of abundance among species ($>1/N$) the species tends to be dominant, thus have lower values of scarcity. Otherwise, species are scarcer when its relative abundance is lower than $1/N$. Thus, scarcity (Sc_i) may be express as:

$$Sc_i = \exp[-N \times \ln(2) \times Ab_i]$$

We also measured species' regional restrictiveness (*R*; Violle *et al.*, 2017), considering species' occurrences in the 40 streams sampled as a measure of geographical extent. R_i is then expressed as 1 minus the geographical extent (*Ge*) of species *i* in comparison to the maximum geographical extent (most widespread species; Ge_{max}). In this way, species with higher values of R have a restricted distribution, while species with lower values are widespread across the region. Thus, regional restrictiveness (R_i) is:

$$R_i = 1 - \frac{Ge_i}{Ge_{max}}$$

To measure functional rarity, we used a local distinctiveness index (*D*) weighted by species' relative abundance, which measures how distinct the species' functional traits are in comparison to all the other species in the same stream. (Violle *et al.*, 2017). Thus, functional distinctiveness (*D*) is the mean functional distance of species *i* to species *j* (d_{ij}) among N other species weighted by its relative abundance (*Ab*), in this way, a species is even more distinct if it does not share its traits with the most abundant species in the community:

$$D_i = \frac{\sum_{j=1,j=i}^{N} d_{ij} \times Ab_j}{\sum_{j=1,j=i}^{N} Ab_j}$$

Regionally, we measured species' functional uniqueness (*U*), which reflects the functional distance of species *i* to species *j* (d_{ij}), in which species *j* is the most functionally similar neighbour of species *i* in the functional space occupied by all species sampled in the region (Violle *et al.*, 2017). In this way, U_i is high when species *i* has a unique combination of traits compared to other species within the region, mainly if the functional distance of species *i* to its closest neighbour is high. Thus, species' restrictiveness (*U*) is:

$$U_i = \min\left(d_{ij}\right) j = i *$$

To calculate the functional rarity indexes, we converted our fuzzy trait matrix to a Gower's distance matrix between species (Pavoine *et al.*, 2009; Grenié *et al.*, 2017). Higher values in Gower's distance represent high differences between pairs of species concerning their functional traits (Pavoine *et al.*, 2009). All the indexes range from 0 to 1, with values closer to 1 representing more scarce, restricted, functionally distinct or unique species (Violle *et al.*, 2017).

Extinction scenarios and data analysis

To assess species extinction's consequences on the functional rarity indexes and the number of functional categories in the community at local and regional scales, we conducted two extinction scenarios. In the first scenario, we ranked species in a decreasing order of *Sc* or *R* and removed scarce or restrict species first, considered the most realistic pattern for the ongoing sixth mass extinction event (Giam *et al.*, 2011; Burkhead, 2012; Pimm *et al.*, 2014). In the second scenario, we ranked species in an increasing order of *Sc* or *R* and removed abundant or widespread species first. This scenario has been described as an unrealistic scenario of extinction (Leitão *et al.*, 2016). However, there is evidence that abundant/widespread species were also extirpated in previous mass extinction events, triggering cascade extinctions on dependent species (Mouillot *et al.*, 2013). We assigned different weights to species by replicating their distinctiveness and traits based on their local abundance and regional occurrence, in this way, abundant and widespread species overcontributes to the functional rarity and it adds redundancy to the traits supported these species (Grime, 1998). Then, we extinguishing individuals at a local scale and populations at a regional scale, instead of species. The average functional rarity (distinctiveness and uniqueness) and the number of remaining functional categories were then calculated for the community after the extinction of each individual/population (Leitão *et al.*, 2016). Then, we defined nine levels (from 10 to 90%) of individuals extinction and extracted the mean functional rarity and number of remaining functional categories from each stream at each extinction level. We conducted null models locally, for each stream, and regionally, for all the streams, to compare with the pattern found in the other extinction scenarios. In the null models, the values of taxonomic rarity (and thus, the order of individuals/populations removal) were shuffled randomly 1000 times while maintaining functional rarity and functional trait values of each individual (Leitão *et al.*, 2016).

Locally, we defined nine levels of extinction, from 10%to 90% of extinction. Then, we computed the average functional rarity and the average number of functional categories for each stream in each extinction level. To identify differences between of the scenarios (scarcest extinct first; most abundant extinct first; and random extinction) at each of the nine extinction levels, we used a non-parametric Friedman-paired test and post-hoc pairwise comparisons (Leitão *et al.*, 2016). Regionally, we computed the confidence interval where 95% of data generated by the null model was confined. Then, we compared this interval with the pattern of functional uniqueness and functional categories loss found in the other two extinction scenarios (most restrict extinct first, and most widespread extinct first). In this way, if the pattern found in the other two extinction scenarios fell out of this confidence interval, we considered the pattern different from the random expectation (Leitão *et al.*, 2016).

All data was analysed in R software (R Core Team, 2020) using the packages vegan (Oksanen, 2019), funrar (Grenié *et al.*, 2017), dplyr (Wickham *et al.*, 2020), ade4 (Dray & Dufour, 2007) and PMCMR (Pohlert, 2014). An R Code with the steps to conduct the analysis is provided in author's account at GitHub (Colares, 2021).

Results

We sampled 14,599 individuals belonging to 57 species, 20 families, and six orders (Appendix S1 – Table D1) in the 40 pristine streams from the Capim basin. The most abundant families were Characidae

(6,899 individuals) and Cichlidae (2,138 individuals), and the most abundant species were *Hyphessobrycon heterorhabdus* (Ulrey, 1894) (6,609 individuals) and *Apistogramma regani* Kullander, 1980 (1520, individuals), which together accounted for more than 50% of the total abundance registered in the study. The most widespread species were *Hyphessobrycon heterorhabdus* (Ulrey, 1894) and *Helogenes marmoratus* Günther, 1863, which both occurred in 39 of the sampled streams. Fourteen species had a local abundance of 3 or less and 13 species occurred in only one stream across the region (Appendix S1 – Table D1). The most redundant functional categories of the diet functional trait were Allochthonous and Autochthonous Invertivores and the Larvivorous category, while the less redundant were Hematophagous, Detritivores, Algivores and Piscivores (Appendix S1 – Figure D1). Local indexes of taxonomic scarcity and functional distinctiveness varied from 0.99 to 0.0002 (mean ± SD = 0.67 ± 0.30) and from 1 to 0.06 (0.47 ± 0.08), respectively (Appendix S1 – Table D1). Regional indexes of taxonomic restrictiveness and functional uniqueness varied from 0.97 to 0.025 (0.40 ± 0.32) and from 0 to 0.77 (0.12 ± 0.16), respectively (Appendix S1 – Table D1).

The simulations to evaluate the effects of extinction on the functional rarity of the community revealed a clear pattern locally: when scarce species were extinct first, the functional distinctiveness of the community decreased, while when abundant species were extinct first, the distinctiveness of the community increased (Fig. 2A). The community's distinctiveness was always different between the extinction scenarios, except for the comparison between the scenarios of scarce species extinction and the random at 10% and 20% of extinction (Fig. 2A). Regionally, the pattern indicated that, when widespread species were extinct first, the functional uniqueness increases above the random expectation (Fig. 2B). On the other hand, when restrict species were extinct first, the uniqueness decreased below the random expectation, but only after 55% populations being extinct (Fig. 2B).

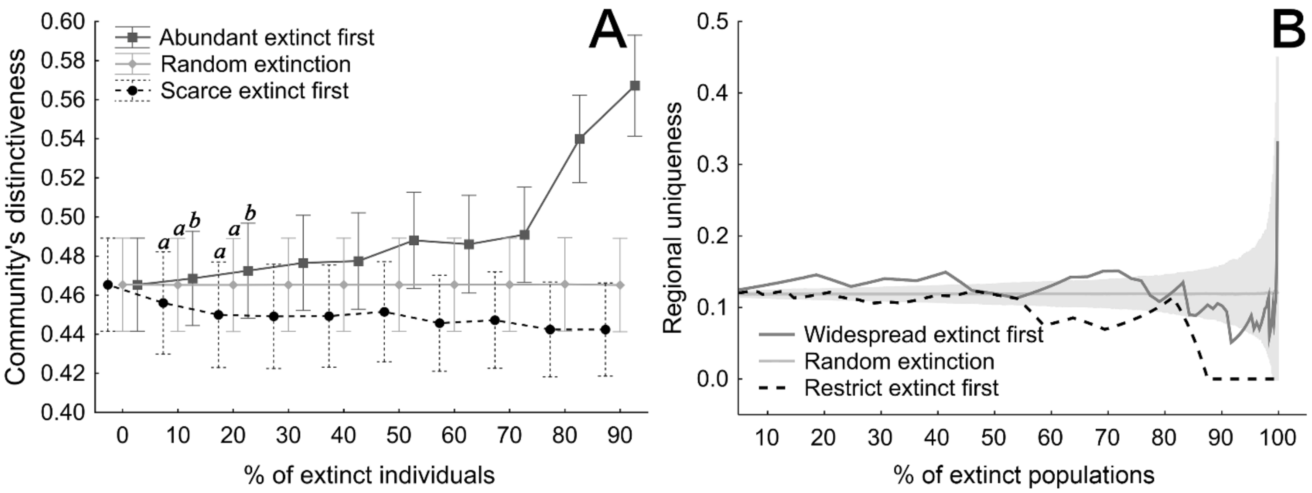

Figure 2. A plot of the mean functional rarity as (A) distinctiveness, at a local scale, and as (B) uniqueness, at a regional scale along with the extinction of individuals/populations in the three extinction scenarios (random extinction, scarce/restrict species extinct first, and abundant/widespread species extinct first). Shapes in the middle are mean values of distinctiveness, and spreads are its 95% confidence intervals. Letters above spreads represent statistically significant differences between the extinction scenarios in each step of extinction at a local scale as returned by the pairwise comparison of the Friedman's tests so that if two scenarios share a letter, they are not different from each other. Scenarios without a letter above spreads indicate statistically significant differences among all three scenarios. (except for 0% of extinct individuals). The grey cloud around the regional random extinction scenario represents confidence intervals as returned by the null model.

The consequences of extinction in the number of functional categories in the community were also evident locally. When scarce species were extinct first, the community lost its first functional category after 5% of extinct individuals and suffered an abrupt loss of four functional categories before the extinction of 50% of individuals (Fig. 4A). The first functional categories lost when scarce species were extinct first were detritivores (in 37.5% of the streams), piscivores (in 32.5% of the streams), algivores (20% of the streams), and hematophagous (10% of the streams) (Fig. 3). While when abundant species were extinct first, the community lost its first functional category only after 90% of extinct individuals (Fig. 4A). The first lost functional categories in this scenario were piscivores (in 40% of the streams), algivores (in 28% of the streams), allochthonous invertivores (in 12% of the streams), hematophagous (in 10%), detritivores (in 8%) and larvivorous (in 2%) (Fig. 3). The number of functional categories in the community was always different between the three scenarios at all extinction levels.

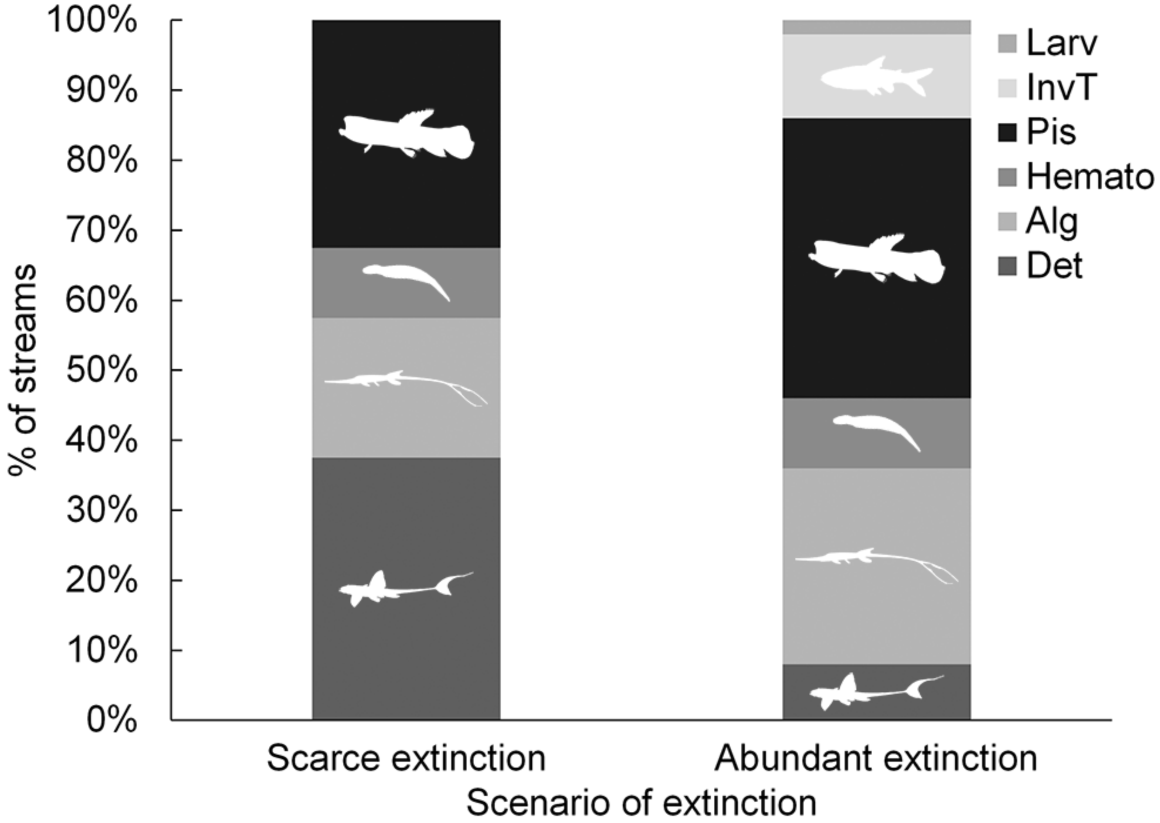

Figure 3. Graphical representation of the first functional categories lost in each of the 40 sampled streams (as percentage of streams in where the functional category was lost first) in both scenarios of non-random extinction (scarce and abundant species extinction). InvA = Autochthonous Invertivore, InvT = Allochthonous Invertivore, Pis = Piscivore, Hemato = Hematophagous, Alg = Algivore, Det = Detritivore, and Larv = Larvivore.

Regionally, when restrict species were extinct first, the loss of functional categories starts near 15% of extinct populations (Fig. 4B), when detritivore fish are lost, followed by a subsequential loss of the hematophagous functional category (Fig. 4B). Posteriorly, the functional categories of algivores, piscivores and autochthonous invertivores are extinct, respectively (Fig. 4B). After 15% of extinction, the pattern of restrict species extinct first was always below the random expectation. On the other hand, the widespread species extinction pattern was never different from the random expectation (Fig. 4B). The first lost functional category in the widespread species extinction scenario was hematophagous (Fig. 4B).

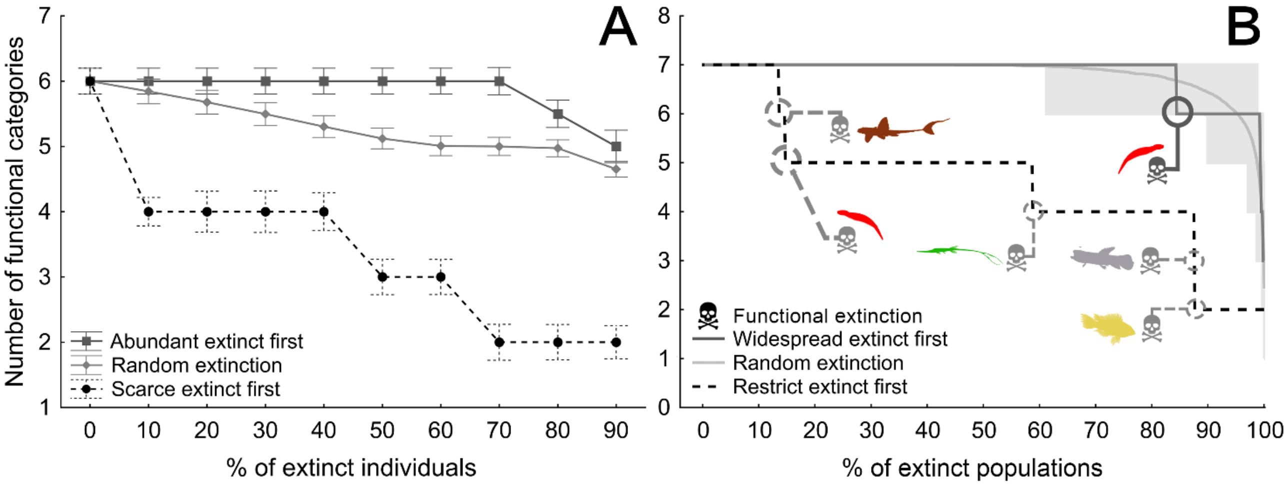

Figure 4. A plot of the number of functional categories after individuals' extinction at (A) local and (B) regional scale in the three extinction scenarios. In the local scale (A), shapes in the middle are median values of the number of functional categories, and vertical bars are 95% confidence intervals. In the regional scale (B), the grey cloud around the random extinction scenario represents confidence intervals of the null model. Grey fish is piscivore, brown is detritivores, green is algivore, reds are hematophagous, and yellow is autochthonous invertivore.

Discussion

Our study evidenced a high contribution of scarce and restrict species in providing distinct and unique functional traits to the ecosystem and community dynamics, corroborating all our hypotheses. Even though functional categories differed in extinction risk, if any of them is extirpated, then cascade effects will occur in the ecosystem through the relationships between the species in the community. The abundance of species that depends on these specific functions may then change, as well as the input of resources such as nutrients in the stream (Hargrave, 2006; Gelwick & Mcintyre, 2017; Reis, Albrecht & Bunn, 2020). Nonetheless, linkages between most species sampled in our study and ecosystem functioning are still not experimentally demonstrated. However, some studies have shown that other tropical stream fish species, which support the same functional categories than the species of our study, have direct and indirect effects on ecosystem functioning (Gilliam *et al.*, 1993; Flecker, 1996; Flecker *et al.*, 2002; Reis *et al.*, 2020).

Some studies have focused on the relationship between rarity and functional loss using indexes (Blackburn *et al.*, 2005; Mouillot *et al.*, 2013; Leitão *et al.*, 2016), such as functional richness or originality, as a proxy for the functional aspects of biological communities (Leitão *et al.*, 2016; Mouillot *et al.*, 2013). Similarly, our study evaluated how the indexes of functional distinctiveness and uniqueness would respond to species extinction in scenarios driven by taxonomic rarity. We found that in both local and regional scales, when scarce and restricted species were extinct first, the community's average distinctiveness tends to decrease as extinction increases. In this way, species with low abundance and restricted geographical distribution overcontribute to the community's functional distinctiveness and uniqueness, providing the most distinct and unique functional traits (Mouillot *et al.*, 2013). In this way, when these species are extinct, the distinctiveness and uniqueness of the community decreases since only abundant and widespread species are left. Otherwise, when species with a high abundance and widespread distribution were extinct first, the community's distinctiveness and uniqueness increased, implying that these species support redundant traits among them. Once abundant species are extinct, only scarce species remain in the habitat, what increases the average functional rarity in the community. Mouillot *et al.* (2013) and Leitão *et al.* (2016) also found a similar pattern as our study for tropical reef and stream fish, trees, and birds, the first using functional distinctiveness and the latter using functional originality, evidencing that rare species often play the most distinct roles in ecosystem functioning.

Regarding the patterns of functional categories loss, when scarce and restrict species were extinct first, the first category was already lost at the begging of the extinction. Human impacts in natural habitats target mainly rare species, most likely to disappear first in the ongoing sixth mass extinction crisis (Pimm *et al.*, 2014). Especially in Amazon, the current land-use expansion is likely to threaten rare species, leading to their local extinctions (Dopheide *et al.*, 2020; Sykes *et al.*, 2020). In most streams, the first functional category lost was detritivores, represented mainly by Siluriformes species such as *Callichthys callichthys*, *Megalechis thoracata*, and *Rineloricaria* sp. If these species are extinct, then we can expect a disruption in nutrient cycling in the stream, as evidenced by Flecker (1996) and Taylor *et al.* (2006) which experimentally showed that after removal of detritivore fish in tropical streams, the downstream transport of organic carbon decreased, while primary production increased (Fig. 5A). This happens because detritivore fish explore the organic matter in the streams, breaking these particles into smaller ones that will be broke by other detritivores in the stream (Taylor *et al.*, 2006). Nevertheless, detritivore fish revolve the substrate of the stream when it is scrapping in stream bottom, releasing particles otherwise locked into the water column (Taylor *et al.*, 2006). It is worth mentioning that, under an extinction scenario triggered by land-use conversion, detritivores may actually benefit from the new environmental conditions of modified streams, since organic matter deposition and algae density are higher than in natural streams (Casatti *et al.*, 2012). This high accumulation of organic matter and algae are resources explored by detritivore fish, which often play a role as detritivore-algivore in streams, thus, these conditions will benefit the persistence of some detritivore species (Casatti *et al.*, 2012). Piscivores were also at significant risk of extinction, represented mainly by Characiformes from the Erythrinidae family (*Erythrinus erythrinus* and *Hoplias malabaricus*), and Siluriformes such as *Batrochoglanis raninus*, *Pimelodella* sp., *Rhamdia muelleri*, and *Tetranematichthys wallacei*. If these fish are extinct, then trophic cascade events may happen in the community due to increases of fishes that will experience a lower predation pressure, such as invertivore fish (Gilliam *et al.*, 1993; Greenberg *et al.*, 2005; Lovell *et al.*, 2017). As the biomass of invertivore fish increases, the predation pressure on invertebrates increases, leading to a lower density of grazing invertebrates, which, in turn, can lead to an overgrowth of algae in the stream (Fig. 5A), as Greenberg *et al.* (2005) experimentally showed for temperate regions. If the environment of a stream is already depleted, then this algae overgrowth could lead to stream eutrophication (Flecker *et al.*, 2002), but this effect is yet to be tested for neotropical streams.

Although we have shown that rare species are at higher risk of extinction and support the most distinct and unique functional traits in the ecosystem, the real impacts of these rare species on ecosystem functioning are still debatable. The "mass ratio hypothesis" postulates that, even though rare species can provide distinct functional traits to ecosystem functioning, their relative importance compared to dominant species are irrelevant (Grime, 1998). Given that rare species often present low abundance and restrict distribution, they might not provide significant contributions to ecosystem functioning when compared to dominant species. Even though we theoretically accounted for the mass ratio hypothesis in our study (as our extinction models extirpate individuals, not species, thus, dominant species overcontributes to ecosystem functioning), we did not directly measure the effects of the species or individuals in the functioning of the stream ecosystem (i.e., direct measures of nutrient released by fish, or direct measurement of predation). Nevertheless, our results concerning the higher extinction risk and functional rarity of scarce and restrict species should not be discarded as it indicates abrupt functional losses that are undeniably linked with ecosystem functioning and community dynamics (Gilliam *et al.*, 1993; Flecker *et al.*, 2002; Taylor *et al.*, 2006; see Table 1 for further information about the effects of each functional category on stream ecosystem). Indeed, several studies have reported that, even though rare species present low abundance and restrict distribution, they still can make significant contributions to the ecosystem, assuring long-term functioning (Lyons *et al.*, 2005; Mouillot *et al.*, 2013). For example, under fluctuations of abundant phytoplankton species over time due to salinity stress, rare species' compensatory growth sustains primary production in a New Zealand lake (Flöder *et al.*, 2010).

In contrast, when locally abundant species were extinct first, functional loss only started after >70% of extinct species. This evidences that these locally abundant species are more resistant to functional loss, given that they occur in high abundance and share their functional traits with many others in the community (Violle *et al.*, 2017). This high redundancy and number of individuals should prevent the extinction of the traits that abundant species provide, ensuring ecosystem functioning and resilience (Purahong *et al.*, 2018; Dopheide *et al.*, 2020). Piscivores and algivores were especially vulnerable to extinction when abundant species were extirpated. The indirect trophic control played by piscivore fish in streams assures an ecosystem with controlled algae density, avoiding eutrophication (Greenberg *et al.*, 2005). Thus, the usage of these fish in biomanipulation programs may help restore eutrophic waters, controlling invertivores fish' biomass, which may increase grazing invertebrates' density, leading to a decrease in the biomass of algae (Greenberg *et al.*, 2005; Lovell *et al.*, 2017). However, this initiative is yet to be tested for tropical streams, even though it has been useful for the restoration of tropical lakes (Jeppesen *et al.*, 2007; Mazzeo *et al.*, 2010). Moreover, the extirpation of algivorous fish (represented by *Farwoella amazonum*, *Nannostomus trifasciatus,* and *Aequidens tetramerus* in this study) should culminate in increases of algae's density (Fig. 5C), further leading to eutrophication through direct extinction of grazing fish as experimentally showed by Flecker *et al.* (2002). Algivore fish also facilitates increases in biomass of nitrogen-fixing cyanobacteria in streams (Power *et al.*, 1988; Flecker, 1996). These fish control diatom algae's biomass, allowing higher biomass of nitrogen-fixing cyanobacteria, which are worse competitors than diatoms (Flecker, 1996). These cyanobacteria fix more atmospheric N when algivore fish are present in the stream, contributing to the input of new nutrients into the aquatic ecosystem (Power *et al.*, 1988; Flecker, 1996).

Regionally, one of the functional categories most vulnerable to extinction was detritivores. Beyond being locally vulnerable, this functional category was also regionally vulnerable when restrict species were extinct first (Fig. 5B). Detritivores contribute to nutrient cycling in the basin and assure downstream transportation of organic carbon. Beyond, they may also overcontribute to nutrient release (of nitrogen and phosphorus) compared to non-detritivores, a fact that reassures the importance of detritivores fish to ecosystem functioning and community dynamics (Sereda, Hudson & McLoughlin, 2008). However, further investigation about the rates of nutrient release by the species found in our study is needed to corroborate such overcontribution in detritivores' nutrient release for Amazonian streams. Another functional category at significant extinction risk is hematophagous, which influences community dynamics by controlling its host population (Fig. 5BD). Specifically, *Paracanthopoma* sp. makes an incision in its host's gills, engorging itself in blood, leaving its host susceptive to diseases and infections, indirectly leading to its death (Spotte, 2002; Zuanon & Sazima, 2005).

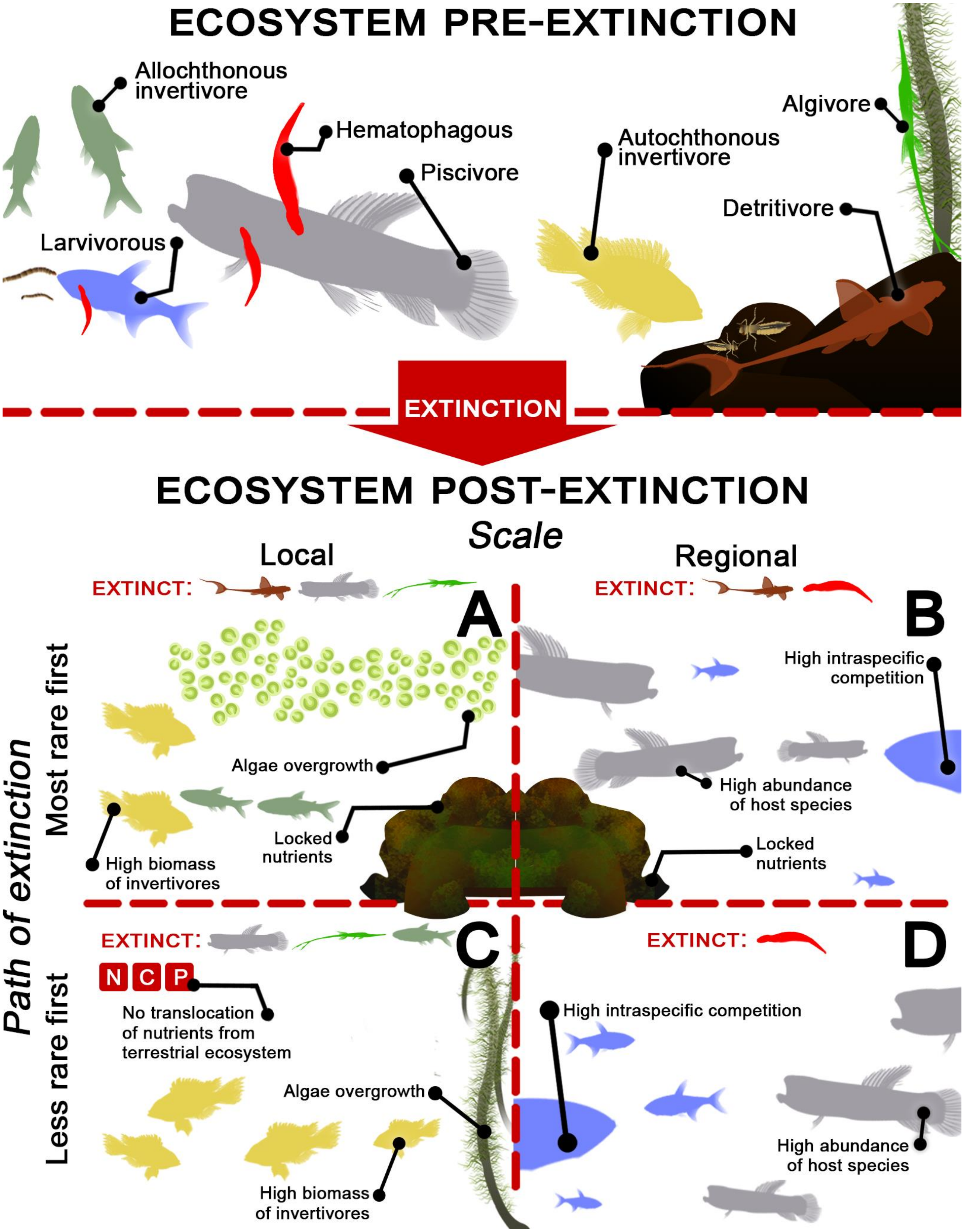
ECOSYSTEM PRE-EXTINCTION
Allochthonous invertivore
Hematophagous
Piscivore
Algivore
Autochthonous invertivore
Detritivore
Larvivorous
EXTINCTION
ECOSYSTEM POST-EXTINCTION
Scale
Local
Regional
Path of extinction
Most rare first
Less rare first
EXTINCT:
A
Algae overgrowth
Locked nutrients
High biomass of invertivores
EXTINCT:
B
High intraspecific competition
High abundance of host species
Locked nutrients
EXTINCT:
C
N
C
P
No translocation of nutrients from terrestrial ecosystem
Algae overgrowth
High biomass of invertivores
EXTINCT:
D
High intraspecific competition
High abundance of host species

Figure 5. Graphical representation of the most vulnerable functional categories in each extinction scenario (represented by the "EXTINCT" fish on the top of A, B, C, and D) and conceptual model of stream ecosystem pre-extinction (on the top) and possible post-extinction scenarios (in the bottom; A, B, C, and D). Pre-extinction (on the top), all functional categories are present in the ecosystem and, once extinction happens (red arrow), the ecosystem functioning changes (in the bottom) due to the extinction of the vulnerable functional categories. The functional categories change regarding its extinction risk depending on the scale, local (A and C) or regional (B and D), and the scenario of extinction, most (A and B) or less rare (C and D) extinct first, with different changes for ecosystem functioning in each of the four possibilities (A, B, C, and D). Grey fish are piscivore, browns are detritivores, vibrant greens are algivores, opaque greens are allochthonous invertivores, reds are hematophagous, and yellows are autochthonous invertivore. Proportions have a ludic purpose only and do not always represent reality.

With these predictions, we may assume that if species' extirpation in the ongoing sixth mass extinction follows the already described pattern of rare (scarce or restrict) species being extinct first, we can expect that Amazonian streams will suffer a rapid functional extinction. Presumably with the establishment of eutrophic ecosystems due to algae overgrowth, a consequence of piscivores and algivores extinction. We may also expect higher intra and inter-specific competition among host species of hematophagous due to parasite extinction. Also, large amounts of organic matter will probably accumulate in the stream bottom, with no release of organic carbon (thus, no downstream transport) due to the extinction of detritivore fish. Throughout this study, we highlight that extinction scenarios driven by taxonomic rarity can predict different functional extinction patterns for fish in Amazonian streams. Thus, our theoretical and analytical approach should be a useful tool for other biological communities.

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Supporting Information

Appendix A: Methods and results of Moran's I

To evaluate whether functional distinctiveness and taxonomic scarcity are spatially structured, we calculated and tested Moran's I (Moran, 1950). First, we generated a matrix of inverse distance weights using the longitude and latitude of each sampled stream. In the matrix, if pairs of points are closer together, then entries are higher than for pairs of samples far apart. We treated the latitude and longitude data as values on a plane, rather than on a sphere, since our sampling points are close together and far from the poles. Then, we calculated Moran's I for each response variable (functional distinctiveness, and taxonomic scarcity) considering a significance level of 0.05. Species composition was represented by the first axis of a Principal Coordinate Analysis (PCoA). Functional distinctiveness and taxonomic scarcity were calculated as described in the main text, then we calculated mean values of distinctiveness and scarcity to each of the 40 samples to conduct Moran's I.

We found that neither functional distinctiveness (computed Moran's I = -0.034, expected Moran's I = -0.026, p = 0.913) nor taxonomic scarcity (computed Moran's I = -0.043, expected Moran's I = -0.026, p = 0.824) were spatially structured.

Appendix B A list of the studies we used to assign the diet functional trait

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Appendix C: Taxonomic composition, total abundance, occurrence, functional trait and its respectively functional categories, and local and regional indexes of the taxonomic and functional rarity.

Table C1. Taxonomic composition, total abundance, occurrence (as the number of streams that the species occurred within the 40 sampled), the proportion of each functional category in the diet for species, and local and regional indexes of the taxonomic and functional rarity of the fish assemblage in the 40 sampled streams. InvA = Autochthonous Invertivore; InvT = Allochthonous Invertivore; Pis = Piscivores; Alg = Algivore; Det = Detritivore; Larv = Larvivorous; Hemato = Hematophagous.

Taxon	Total Abundance	Occur-rence	Diet fuzzy trait							Local rarity indexes		Regional rarity indexes	
			InvA	InvT	Pis	Alg	Det	Larv	Hemato	Scarcity	Distinctiveness	Restrictiveness	Uniqueness
CHARACIFORMES													
Characidae													
Bario steindachneri (Eigenmann, 1893)	3	3	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.96	0.68	0.93	0.00
Hemigrammus belottii (Steindachner, 1882)	217	11	0.00	0.74	0.00	0.00	0.00	0.26	0.00	0.56	0.47	0.73	0.18
Hemigrammus rodwayi Durbin, 1909	45	6	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.78	0.35	0.85	0.00
Hyphessobrycon heterorhabdus (Ulrey, 1894)	6609	39	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.16	0.42	0.03	0.00
Knodus victoriae (Steindachner, 1907)	8	2	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.68	0.43	0.95	0.00
Moenkhausia collettii (Steindachner, 1882)	7	3	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.93	0.28	0.93	0.00
Moenkhausia oligolepis (Günther, 1864)	9	5	0.16	0.48	0.06	0.05	0.01	0.24	0.00	0.97	0.38	0.88	0.19
Phenacogaster pectinatus (Cope, 1870)	1	1	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.87	0.60	0.98	0.00
Crenuchidae													
Characidium etheostoma Cope, 1872	65	14	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.85	0.84	0.65	0.27
Characidium zebra Eigenmann, 1909	1	1	0.42	0.01	0.01	0.00	0.00	0.56	0.00	0.87	0.61	0.98	0.08
Crenuchus spilurus Günther, 1863	25	4	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.92	0.42	0.90	0.00
Melanocharacidium dispilomma Buckup, 1993	1	1	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.87	0.60	0.98	0.00
Microcharacidium weitzmani Buckup, 1993	732	17	0.25	0.00	0.00	0.00	0.00	0.75	0.00	0.48	0.54	0.58	0.05
Erythrinidae													
Erythrinus erythrinus (Bloch & Schneider, 1801)	497	38	0.13	0.25	0.50	0.00	0.00	0.13	0.00	0.69	0.75	0.05	0.35
Hoplias malabaricus (Bloch, 1794)	47	17	0.18	0.00	0.82	0.00	0.00	0.00	0.00	0.86	0.95	0.58	0.15

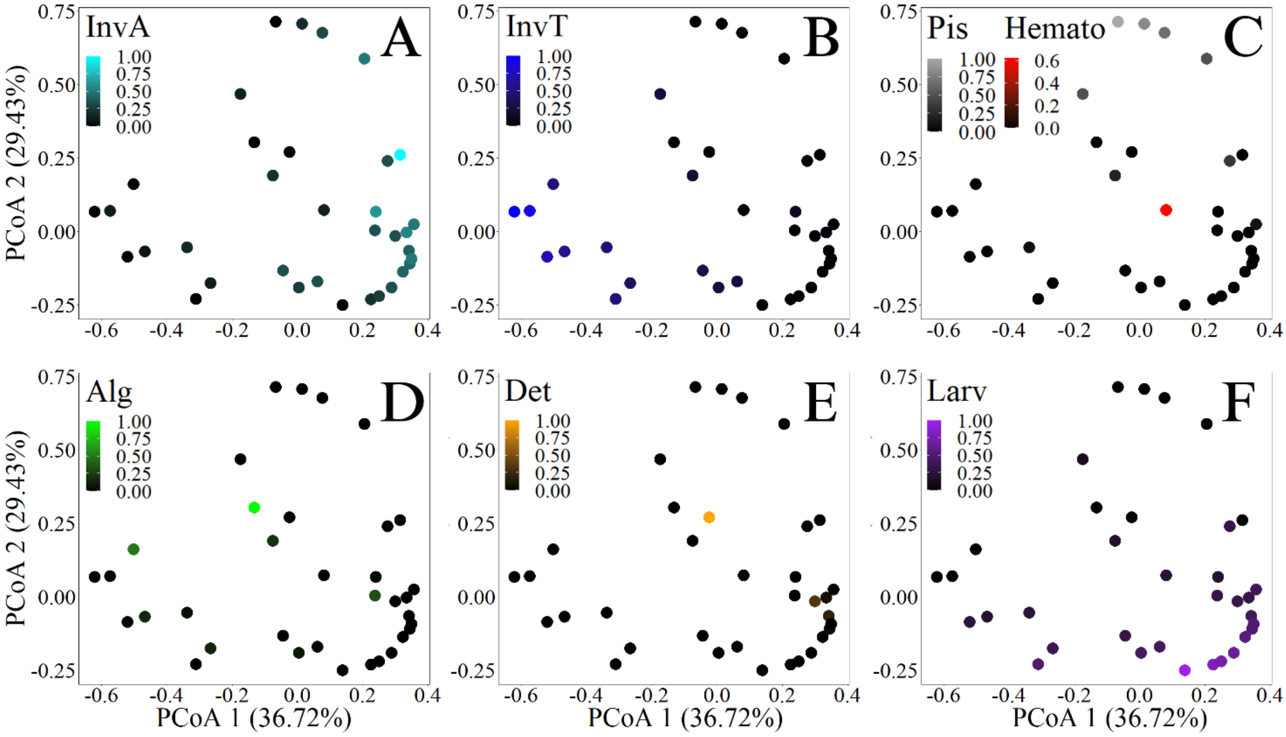
Gasteropelecidae													
Carnegiella strigata (Günther, 1864)	8	2	0.10	0.90	0.00	0.00	0.00	0.00	0.00	0.68	0.62	0.95	0.08
Iguanodectidae													
Bryconops caudomaculatus (Günther, 1864)	1	1	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.93	0.37	0.98	0.00
Iguanodectes rachovii Regan, 1912	927	25	0.07	0.57	0.00	0.14	0.00	0.21	0.00	0.35	0.51	0.38	0.18
Lebiasinidae													
Copella arnoldi (Regan, 1912)	323	10	0.11	0.39	0.00	0.14	0.00	0.36	0.00	0.41	0.39	0.75	0.23
Nannostomus trifasciatus Steindachner, 1876	47	10	0.33	0.00	0.00	0.33	0.00	0.33	0.00	0.84	0.67	0.75	0.43
Pyrrhulina brevis Steindachner, 1876	909	38	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.62	0.29	0.05	0.00
CICHLIFORMES													
Cichlidae													
Aequidens tetramerus (Heckel, 1840)	214	29	0.00	0.50	0.00	0.50	0.00	0.00	0.00	0.82	0.75	0.28	0.45
Apistogramma regani Kullander, 1980	1520	37	0.33	0.25	0.00	0.00	0.00	0.42	0.00	0.33	0.48	0.08	0.00
Apistogramma agassizii (Steindachner, 1875)	118	3	0.25	0.25	0.00	0.08	0.00	0.42	0.00	0.46	0.37	0.93	0.14
Crenicichla saxatilis (Linnaeus, 1758)	128	19	0.50	0.00	0.10	0.00	0.00	0.40	0.00	0.76	0.63	0.53	0.13
Nannacara taenia Regan, 1912	158	7	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.53	0.47	0.83	0.10
CYPRINODONTIFORMES													
Rivulidae													
Anablepsoides urophthalmus (Günther, 1866)	347	35	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.77	0.59	0.13	0.17
GYMNOTIFORMES													
Gymnotidae													
Gymnotus carapo Linnaeus, 1758	7	6	0.55	0.04	0.00	0.00	0.07	0.33	0.00	0.96	0.68	0.85	0.17
Gymnotus coropinae Hoedeman, 1962	213	32	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.77	0.62	0.20	0.00
Gymnotus pantherinus (Steindachner, 1908)	115	24	0.62	0.14	0.00	0.03	0.00	0.22	0.00	0.79	0.68	0.40	0.19
Gymnotus sp.	2	1	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.93	0.50	0.98	0.00
Hypopomidae													
Brachyhypopomus beebei (Schultz, 1944)	70	8	0.20	0.00	0.00	0.00	0.00	0.80	0.00	0.89	0.55	0.80	0.00
Brachyhypopomus brevirostris (Steindachner, 1868)	27	5	0.20	0.00	0.00	0.00	0.00	0.80	0.00	0.83	0.42	0.88	0.00
Brachyhypopomus sp.2	210	21	0.20	0.00	0.00	0.00	0.00	0.80	0.00	0.80	0.53	0.48	0.00
Brachyhypopomus sp.3	11	5	0.20	0.00	0.00	0.00	0.00	0.80	0.00	0.92	0.46	0.88	0.00
Brachyhypopomus sp.4	4	1	0.20	0.00	0.00	0.00	0.00	0.80	0.00	0.73	0.48	0.98	0.00

Hypopygus lepturus Hoedeman, 1962	18	7	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.89	0.57	0.83	0.00
Microsternarchus bilineatus Fernández-Yépez, 1968	29	9	0.33	0.25	0.00	0.00	0.00	0.42	0.00	0.88	0.38	0.78	0.00
Rhamphichthyidae													
Gymnorhamphichthys petiti Géry & Vu, 1964	320	19	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.52	0.42	0.53	0.00
Sternopygidae													
Eigenmannia sp.	1	1	0.40	0.00	0.00	0.00	0.20	0.40	0.00	0.96	0.54	0.98	0.19
Sternopygus macrurus (Bloch & Schneider, 1801)	1	1	0.45	0.00	0.00	0.00	0.05	0.50	0.00	0.97	0.59	0.98	0.06
SILURIFORMES													
Auchenipteridae													
Tetranematichthys wallacei Vari & Ferraris, 2006	1	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.97	0.99	0.98	0.00
Callichthyidae													
Callichthys callichthys (Linnaeus, 1758)	6	5	0.33	0.00	0.00	0.00	0.33	0.33	0.00	0.98	0.72	0.88	0.00
Corydoras melanistius Regan, 1912	3	1	0.20	0.20	0.20	0.20	0.00	0.20	0.00	0.66	0.59	0.98	0.00
Megalechis picta (Müller & Troschel, 1849)	1	1	0.20	0.20	0.20	0.20	0.00	0.20	0.00	0.97	0.57	0.98	0.00
Megalechis thoracata (Valenciennes, 1840)	2	2	0.33	0.00	0.00	0.00	0.33	0.33	0.00	0.97	0.67	0.95	0.00
Cetopsidae													
Denticetopsis epa Vari, Ferraris & de Pinna, 2005	14	9	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.90	0.62	0.78	0.00
Helogenes marmoratus Günther, 1863	409	39	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.70	0.30	0.03	0.00
Doradidae													
Acanthodoras cataphractus (Linnaeus, 1758)	1	1	0.33	0.00	0.33	0.00	0.00	0.33	0.00	0.97	0.65	0.98	0.33
Heptapteridae													
Mastiglanis asopos Bockmann, 1994	7	2	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.80	0.39	0.95	0.00
Pimelodella sp.	6	5	0.30	0.02	0.68	0.00	0.00	0.00	0.00	0.94	0.90	0.88	0.15
Rhamdia muelleri (Günther, 1864)	12	5	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.89	0.95	0.88	0.00
Loricariidae													
Farlowella amazonum (Günther, 1864)	11	5	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.82	0.95	0.88	0.54
Rineloricaria sp.	1	1	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.87	1.00	0.98	0.65
Pseudopimelodidae													
Batrochoglanis raninus (Valenciennes, 1840)	5	3	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.87	0.84	0.93	0.26
Trichomycteridae													
Ituglanis sp.	100	19	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.80	0.33	0.53	0.00

Paracanthopoma sp.	25	7	0.13	0.00	0.00	0.00	0.00	0.25	0.63	0.84	0.86	0.83	0.77

Appendix D: Figure of the functional space occupied by the species sampled.

Figure D1. Axis of a Principal Coordinates Analysis representing the functional space occupied by the traits of the 57 species sampled in our study. Each colour gradient represents the proportion of species' diet to the functional category of trait. InvA = Autochthonous Invertivore, InvT = Allochthonous Invertivore, Pis = Piscivore, Hemato = Hematophagous, Alg = Algivore, Det = Detritivore, and Larv = Larvivore.



Habitat loss and fish functional extinction in Amazonian streams in the Anthropocene

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Habitat loss and the fish functional extinctions in Amazonian streams in the Anthropocene

Abstract

Earth has entered a sixth mass extinction event during the Anthropocene and its major cause is the habitat loss promoted by human activities. In this context, rare species that survive only under high habitat integrity are the main target of extinction. Extinction will bring cascade effects to ecosystem functioning when functional losses occur in the habitat. In this view, our main goal was to predict and scale future scenarios of functional extinction in Amazonian streams. We investigated the effects of fish species extinction in functional rarity and individual functional traits at local and regional scales, further identifying the traits prone to extirpation. We sampled the fish community and environmental conditions of 63 streams at eastern Amazon. Then, we built an integrated index of vulnerability to extinction based on species' rarity and vulnerability to habitat loss, in which rare species that survive only under high habitat integrity are sensible, and common species that supports low habitat integrity are tolerant. Finally, we constructed three extinction scenarios that extirpated (I) sensible, (II) and tolerant species, and (III) at random. We found that when sensible species to habitat loss were extinct first, the functional rarity of the community decreased at local scale, but increased at regional scale, while when tolerant species were extinct first, we registered the inverse pattern. Moreover, functional losses start after the extinction of 5% and 10% of sensible species at local and regional scales, respectively. In contrast, tolerant species supports 90% and 95% of extinction until the first functional loss occur at local and regional scales, respectively. If the ongoing extinction crisis indeed targets sensible species, we should expect that Amazon stream ecosystem will collapse under rapid functional loss after the extinction of piscivores, detritivores, algivores and hematophagous, the most vulnerable traits.

Keywords: effect traits; functional rarity; land-use; deforestation; trophic ecology.

Introduction

Habitat loss happens when a natural habitat is destroyed or heavily altered into a new habitat with different resources and conditions than previously available, thus, an area that is no longer able to support the species that previously composed the community (Bueno et al. 2018). This process is one of the major threats to biodiversity in the Anthropocene, often leading to species extinction and further changes in ecosystem and community dynamics (Pimm et al. 2014, Bueno et al. 2018). However, different species may show distinct responses to habitat loss. Some species have a broad dietary breadth and are able to thrive in several habitats with different environmental conditions, these are tolerant species: they are less prone to extinction since they are able to support altered conditions or to explore the resources after habitat loss (McKinney and Lockwood 1999, Bueno et al. 2018). Otherwise, some species have evolved exploring specific diets or tolerating a small range of conditions in pristine environments, these are sensible species: they are more prone to extinction after habitat loss since they depend on specific conditions and resources provided only by pristine habitats (McKinney and Lockwood 1999, Bueno et al. 2018).

Once species are extinct, the function they provided to ecosystem and community maintenance also disappears if no other species continues to provide the same function in the ecosystem (Violle et al. 2017). The risk of functional extinction after habitat loss depends not only on if species are sensible or tolerant but also on their taxonomic and functional rarity (Violle et al. 2017, Bueno et al. 2018). Populations composed by few individuals and species distributed in a restrict area should be at higher risk of extinction than populations of abundant species with a widespread distribution, since few individuals or populations need to go extinct for the species to disappear regionally (Hull et al. 2015, Violle et al. 2017). Concerning their functional rarity, species may provide redundant functions when several species perform similar ecological functions in the ecosystem, or distinct functions when species provide an exclusive function in the ecosystem (Naeem 1998, Violle et al. 2017). Distinct and unique functions to the ecosystem are usually provided by sensible species. In this view, the extinction of some redundant species might not have relevant consequences to ecosystem functioning since remaining species still provide the same function (Violle et al. 2017).

Pristine forests in Amazon have been converted into cattle ranching and monocultures recently but in an increasing rate (TerraBrasilis 2020), which led to a loss of nearly 20% of natural habitats in Amazon (Zemp et al. 2017). Rates of deforestation are increasing (TerraBrasilis 2020) and threatening especially sensible and rare species to extinction (McKinney and Lockwood 1999, Hubbell 2013, Foley et al. 2014, Zemp et al. 2017). If these species support distinct functions in the ecosystem, then we should expect the disappearance of essential goods and services provided by the Amazon rainforest. Although habitat loss due to deforestation is most noticeable in terrestrial habitats, freshwater streams are also depleted given its dependencies from the terrestrial habitat in its margins (Casatti et al. 2012, Azevedo-Santos et al. 2019). The pervasive effects of habitat loss in aquatic environments are expressed as losses in stream’ integrity, such as changes in the environmental conditions and loss of resources (such as food and microhabitats; Prudente et al. 2018). Moreover, species may respond to habitat loss changing from a diverse community supporting several ecosystem functions to a community composed by tolerant and functionally redundant species (McKinney and Lockwood 1999, Flynn et al. 2009).

In this view, our main goal is to predict and scale future effects of species extinction on ecosystem functioning in scenarios of extinction driven by species' vulnerability to habitat loss. To do so, we developed three extinction scenarios of (1) sensible and (2) tolerant species to habitat loss extinction and a (3) random extinction scenario to answer three major questions: (a) How the functional rarity of the community changes as species goes extinct based on their vulnerability to habitat loss at local and regional scales? (b) How many individuals, at the local scale, and populations, at the regional scale, need to be extinct in each scenario for the community to lose its first function at both scales? And (c) which is the first lost functional category in the different extinction scenarios? We hypothesize that when sensible species to habitat loss are extinct first, the community's functional rarity should decrease as species go extinct, and the first function should be lost after few species go extinct. Otherwise, when tolerant species to habitat loss are extinct first, the community's functional rarity should increase as species go extinct, and the first function should be lost after many species went extinct. Sensible species usually provide a set of distinct and unique functions to the ecosystem (Birkhofer et al. 2015, Violle et al. 2017); thus, when they go extinct, the community's functional rarity should decrease as only tolerant species remain in the community, which are usually functionally redundant (Casatti et al. 2015a, Violle et al. 2017).

Methods

We sampled 63 first to third order streams in the Capim river basin, eastern Amazon, from 2012 to 2018 (Fig. 1). The region has a humid-tropical climate, with a rainy period from December to May, and a dry period from June to November. The mean annual temperature reaches 26°C e the mean annual precipitation is 2344 mm^3, reaching a maximum of 427 mm^3 during May, and a minimum of 54 mm^3 during September. Streams were sampled during the dry season to avoid seasonal variation among samples and selected based on their accessibility, assuring the independence between samples by always sampling streams at least 2 km far from each other following the watercourse. The region is a mosaic of cities, agriculture and cattle ranching due to extensive human exploitation, but still, a portion of its territory is composed by large pristine forest fragments (Fig. 1).

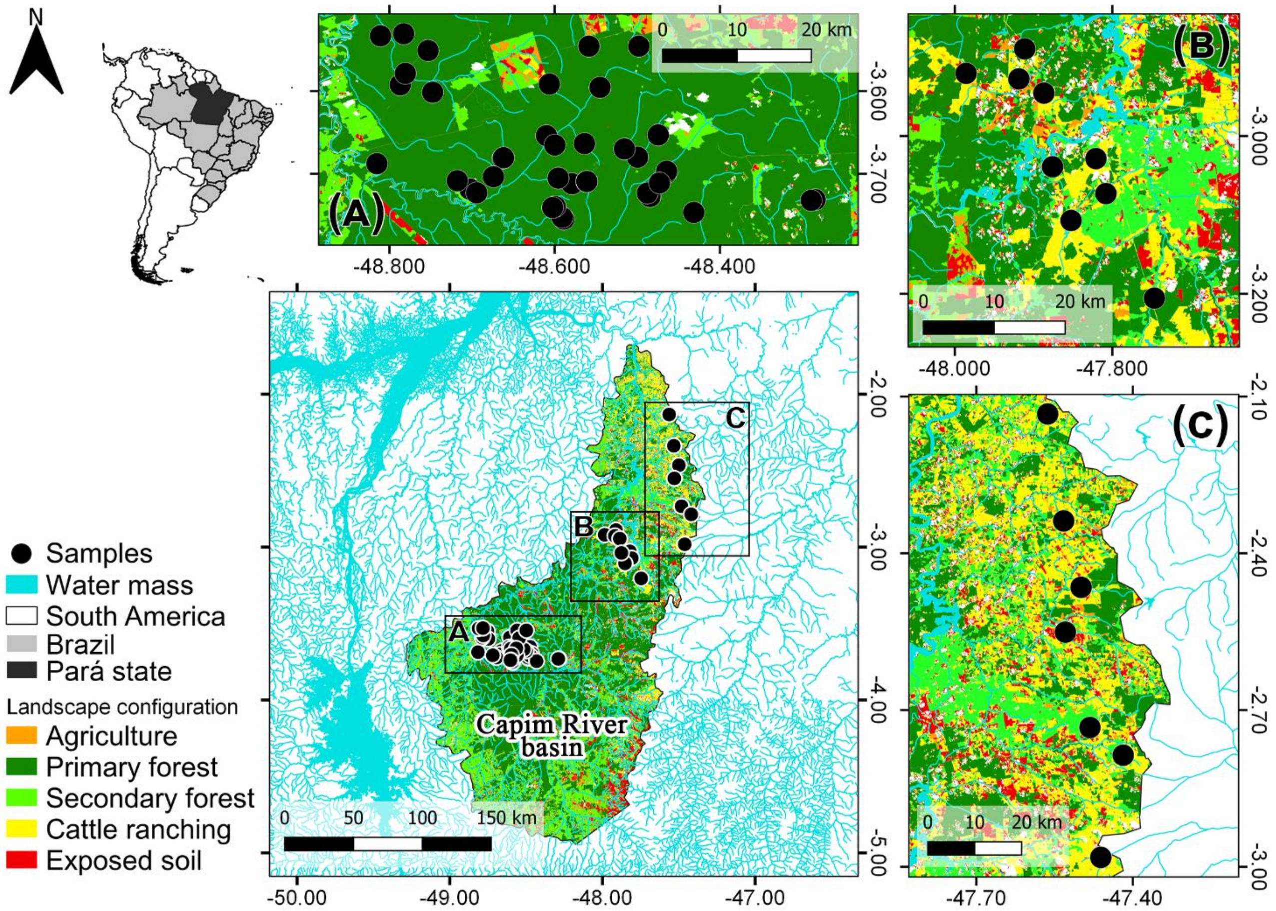

Figure 1. The geographical location of the 63 sampled streams and landscape configuration in Capim River basin, eastern Amazon.

We sampled fishes using hand nets during six hours in a stretch of 150 m of each stream. This active sampling method assures high sampling efficiency, since we are able to sample the majority of microhabitats used by Amazon stream fish (Leitão et al. 2016; Montag et al. 2019). The collected fish were euthanized with lethal doses of Eugenol anaesthetic, fixed in Formalin at 10% concentration and after a 72 hours period, fishes were conserved in Alcohol at 70% concentration for further identification. In the laboratory, fishes were counted and identified to the lowest taxonomical level possible using specialized literature (Albert 2001, Reis et al. 2003, Van der Sleen and Albert 2018) and with the help of fish taxonomists. The Animal Ethics Committee (CEUA) approved the collecting method) under protocol number 8293020418 (UFPA).

In each of the 63 streams, we measured seven environmental variables previously reported to influence stream fish (Juen et al. 2016, Prudente et al. 2017, Ferreira and Begot 2018, Montag et al. 2019) following the method proposed by Peck et al. (2006) with metric calculations following Kaufmann et al. (1999).: (I) Mean depth of thalweg (cm), (II) standard deviation (SD) of thalweg depth (cm), (III) fast channel habitats (%), (IV) SD canopy density stands (%), and (V) proportion of human impact, which increases in human modified habitats, and (VI) mean woody cover, and (VII) proportion of undercut banks, which decreases in human modified habitats. We measured thalweg in 150 equidistant measures of depth along the thalweg profile, when was also recorded the occurred of undercut banks and classified the channel habitat type (into pool, smooth flow, riffle, rapid, cascade, waterfall or dry channel). Posteriorly, we considered riffle, rapid, cascade and waterfall into fast channel habitats and calculated the proportion of fast channel habitats in comparison to other channel habitat types. In addition, we subdivided the 150 m stretch of the stream into 10 equidistant subsections and established a 10 m² plot adjacent to each subsection to evaluate the structure and density of riparian vegetation. Then, we measured canopy and woody cover in each plot using a densitometer in six directions: centre-upstream, centre-downstream, centre-left, centre-right, left and right. In each subsection, we visually assessed the presence of and proximity to human disturbances in both riverbanks, quantifying the occurrence of land uses or anthropogenic disturbances (i.e., plantation, pasture, logging, mining, walls, dykes, canals, dams, buildings, pavement, roads, railroads, drainage pipes, landfill/trash, and parks). The observations were assigned to one of three proximity classifications: B, within the stream or in the margins; C, within the riparian plot; P, outside the riparian plot; and 0, for no human disturbance.

We assigned a functional trait of species' diet divided into seven functional categories: (I) Autochthonous invertivore (feed on adult forms of aquatic invertebrates); (II) allochthonous invertivore (feed on adult forms of terrestrial invertebrates); (III) piscivore (feed on other fish); (IV) algivore (feed on algae); (V) larvivorous (feed on the larvae of aquatic and some terrestrial organisms);

(VI) detritivore (feed on organic matter in the bottom of stream); and (VII) hematophagous (feed on blood). The diet trait is a fuzzy-type, since it is based on the proportions of each functional category, and was chosen because of its ability to inform the *effect* of functional extinction in the ecosystem dynamics (Table 1; Violle et al. 2007, Pavoine et al. 2009).

Table 1. Diet functional trait, its respective categories (functions), and why they are important in ecosystem functioning and community dynamics. Information from the "Why is this function important?" and its references support the post-extinction scenario of functions in Fig. 5.

Functional effect trait	**Categories**	**Why is this function important?**
DIET	Autochthonous invertivore	These are fish who feed on adult aquatic invertebrates. When autochthonous invertivore fish are present in the stream, they control the population of grazing invertebrates, thus lowering the predation pressure on periphytic algae (Hargrave et al. 2006). This top-down control allows higher algae biomass and higher primary production in the ecosystem (Hargrave 2006). Beyond, Hargrave et al. (2006) indicates that when autochthonous invertivore fish decreases the density of grazing invertebrates, it leads to lower competition among grazer species, allowing for higher growth of grazer fish.
	Allochthonous invertivore	These are fish who feed on adult terrestrial invertebrates. They actively translocate nutrients between terrestrial and aquatic ecosystems, providing "new" nutrients in the stream (Vanni 2002). This enhanced nutrient input allows for higher primary productivity, thus more complex trophic interactions and higher densities of consumers (Hargrave 2006). In this view, ecosystems where this function is played by fish usually present higher primary and secondary productivity (Nakano and Murakami 2001).
	Piscivore	These fish directly control the population of its prey. Experimental studies have previously related cascade trophic effects of these predatory fish on invertivores fish biomass and growth (Gilliam et al. 1993, Greenberg et al. 2005, Lovell et al. 2017). Gilliam et al. (1993) evidenced that the presence of the piscivore *Hoplias malabaricus* led to lower biomass of a preyed invertivorous fish in tropical streams, which only presented small individuals in sites where the predator was present.
	Algivore	These are fish who feed on phytoplankton or periphytic algae. They control the algae population in streams, allowing the coexistence between species and higher diversity of algae (Power et al. 1988, Flecker

	1996). When algivore fish are present, the biomass of diatoms tends to decrease while the biomass of nitrogen-fixing cyanobacteria increases, as these cyanobacteria are facilitated by algivores (Power et al. 1988, Flecker 1996). The extinction of this functional category can trigger a eutrophication process in the stream if environmental conditions are already degraded, creating a hypoxic system with low visibility and water quality due to algae overgrowth (Flecker et al., 2002).
Detritivore	These are fish who explore the organic matter accumulated in the stream bottom. They assure the nutrient cycling in the ecosystem, releasing the organic carbon locked in the organic matter in the ecosystem to be used by other organisms in the trophic web (Flecker 1996, Taylor et al. 2006). Beyond interfering in its stream, detritivore species also ensure the release of organic carbon downstream, as the nutrient is carried by streamflow (Taylor et al. 2006).
Larvivorous	These fish control the population of its larvae prey, influencing the adult population densities of these organisms (Wesner 2010). Experimental studies have shown that the effects that larvivorous fish may have in the community cross boundaries of ecosystems, for example, fish who feed on Dragonfly and Mosquito aquatic larvae decreases the population of the insects in the adult phase, at the terrestrial habitat (Chandra et al. 2008, Wesner 2010). Larvivorous fish are effectively at controlling the biomass of Mosquitos that are vectors of human diseases, such as malaria and dengue fever, common diseases in the tropics (Chandra et al. 2008, De Góes Cavalcanti et al. 2009).
Hematophagous	These fish feed on the blood of other fish, making an incision on the gills arteries and engorging themselves in the blood (Zuanon and Sazima 2004). They can kill its host (although it is rare) but mainly makes its host more vulnerable to diseases and infections due to the open incision they left in the host's blood system (Spotte 2002, Zuanon and Sazima 2004). As hematophagous weakens its host and indirectly leads to its death is an important function itself, as it contributes to nutrient cycling by leaving its host body to be decomposed. Beyond, the death of the host reduces intraspecific competition among its host in the stream, allowing the coexistence of multiple species. The species in our study (*Paracanthopoma* sp.) uses its host to migrate between water bodies, in this way, this hematophagous contributes to the input of "new" translocate nutrients between streams and rivers trough excretion (Zuanon and Sazima 2005).

To accurately assign species' diet, we conducted digestive tract content analysis combined with a literature search of species' diet. To analyse species' digestive tracts, we selected six individuals of each species (except for those with less than six individuals) with similar body sizes to avoid ontogenetic variation. We then removed the digestive tract through a ventral incision. Further, we dissected the digestive tract, and its content was screened and identified to the lowest taxonomical level possible using specific literature (Mugnai et al. 2010, Hamada et al. 2014) and the help of specialists in the different taxonomic groups. Finally, we measured the proportion (%) of each functional category for each species based on the food items found in its digestive tract (Hyslop 1980). To complement the digestive tract analyses, we collected published studies that assigned proportions of food items for the species. Moreover, we summed this diet proportion based on the literature to those based on digestive tract analyses. For studies that classified species into trophic groups instead of providing diet proportions, we assigned equal proportions of functional categories based on each trophic group cited by the study. We considered only studies that described the diet of adult stages of species. When we did not find diet literature to a specific species and to species which we only identified to genus level, we considered studies that described the diet of other species from the genus.

Data analysis

We measured functional rarity at local and regional scales, as distinctiveness (*D*) and uniqueness (*U*) indexes, respectively (Violle et al. 2017). To measure functional rarity, we used a local distinctiveness index (*D*) weighted by species' relative abundance, which measures how distinct the species' functional traits are in comparison to all the other species in the same stream. (Violle *et al.*, 2017). Thus, functional distinctiveness (*D*) is the mean functional distance of species *i* to species *j* (d_{ij}) among N other species weighted by its relative abundance (*Ab*), in this way, a species is even more distinct if it does not share its traits with the most abundant species in the community:

$$D_i = \frac{\sum_{j=1,j=i}^{N} d_{ij} \times Ab_j}{\sum_{j=1,j=i}^{N} Ab_j}$$

Regionally, we measured species' functional uniqueness (*U*), which reflects the functional distance of species *i* to species *j* (d_{ij}), in which species *j* is the most functionally similar neighbour of species *i* in the functional space occupied by all species sampled in the region (Violle et al. 2017). In this way, U_i is high when species i has a unique combination of traits compared to other species within the region, mainly if the functional distance of species i to its closest neighbour is high. Thus, species' restrictiveness (U) is:

$$U_i = \min\left(d_{ij}\right) j = i *$$

To calculate the functional rarity indexes, we converted our fuzzy trait matrix to a Gower's distance matrix between species (Pavoine et al. 2009, Grenié et al. 2017). Higher values in Gower's distance represent high differences between pairs of species concerning their functional traits (Pavoine et al. 2009).

To measure taxonomic rarity, we used a local scarcity index (*Sc*), which is the inverse of species' relative abundance, but it ranges from 0 to 1 and has a pivotal value of 0.5 for species with a relative abundance corresponding to *1/N*, as *N* is the number of species in the community (Violle et al. 2017). When the relative abundance of species i (Ab_i) is higher than its expectation under a perfect evenly distribution of abundance among species (>*1/N*) the species tends to be dominant, thus have lower values of scarcity. Otherwise, species are scarcer when its relative abundance is lower than *1/N*. Thus, scarcity (Sc_i) may be express as:

$$Sc_i = \exp[-N \times \ln(2) \times Ab_i]$$

We also measured species' regional restrictiveness (*R*; Violle et al. 2017), considering species' occurrences in the 40 streams sampled as a measure of geographical extent. R_i is then expressed as 1 minus the geographical extent (*Ge*) of species i in comparison to the maximum geographical extent (most widespread species; Ge_{max}). In this way, species with higher values of *R* have a restricted distribution, while species with lower values are widespread across the region. Thus, regional restrictiveness (R_i) is:

$$R_i = 1 - \frac{Ge_i}{Ge_{max}}$$

We choose to assess rarity in local and regional scale because species can vary regarding its rarity according to the scale (Violle et al. 2017). For instance, a species can provide exclusive traits to the local stream, but when we consider the whole basin, the same species may share its traits with others of different streams.

To determine species' vulnerability to habitat loss, we first measured the habitat integrity of each sample based on the seven environmental variables collected. Habitat integrity should reflect "how much" of that habitat is already lost as long as habitat integrity is based on environmental variables that vary according to human modification (Prudente et al. 2018). Thus, to calculate the habitat integrity, first standardized the environmental variables on a continuous scale ranging from 0 (lowest integrity possible) to 10 (highest integrity possible) using the lower and upper expectation of interquartile range (Klemm et al. 2003). The upper limit was defined as the 75th percentile of the distribution of the variable, while the lower limit was the 25th percentile of the distribution of the variable. Values higher than the upper limit received a value of 10, while those under the lower limit received a value of 0. All other values were standardized based on the equation: Standardized variable = observed value – lower limit/upper limit – lower limit. For variables that increased in human disturbed streams, we corrected the index based on: Corrected index = (calculated index – 10) * (-1). With this correction, all variables increase as habitat integrity increases. Finally, for each stream, the final value of habitat integrity was obtained through the sum of all seven standardized variables divided by the number of variables.

Moreover, we used the minimal habitat integrity needed for species to survive as a measure of sensibility to habitat loss. In this way, if the minimal integrity needed for a species to survive is 0, it should be more tolerant to habitat loss. Whereas, if the minimal integrity needed for a species to survive is 10, then it should be more sensible to habitat loss, since it only survives under high habitat integrity. We identified this minimal integrity needed for species with >3 occurrences using a Threshold Indicator Taxa Analysis (TITAN; with 999 permutations) of species' abundance against the habitat integrity gradient (King and Baker 2014). For those with <3 occurrences, we used the lowest habitat integrity in which the species occurred in the streams.

To develop simulations of extinction driven by species' vulnerability to habitat loss, we built an additional framework that considered species rarity and its minimal habitat integrity needed to survive. We first standardized the minimal habitat integrity needed for species to survive to range from 0 to 1 so we could sum with species' rarity, divide by two, and construct a single index that summarized species' rarity and sensibility to habitat loss. This new index of vulnerability to habitat loss ranges from 0, for tolerant species, which are abundant at local scale or widespread at regional scale, and able to survive under low habitat integrity, to 1, for sensible species, which are scarce (local scale) or restrict (regional scale) and survive only under high habitat integrity. We built simulations of extinction in which the individuals, in the local scale, and populations, at the regional scale, were extinct based on species' vulnerability to habitat loss. In this view, we built three extinction scenarios in each scale: (I) tolerant species extinct first, (II) sensible species extinct first, and (III) random extinction. We built the random scenario to compare with the other two scenarios (sensible and tolerant species extinction). The random scenario is based on null models for each stream, at local scale, and for all samples, at the regional scale, that randomized species' vulnerability to habitat loss (thus, the order of extinction) 1000 times while conserving species' functional rarity and functional traits (Leitão et al. 2016). Our extinction scenarios also return an ordered list from the first to the last functional category lost after extinction. Thus, to answer our third question, we identified the order of functional category extinction, at the regional scale, and the proportion (%) of the first lost functional category considering each stream at the local scale.

To test for differences in functional rarity, associated with our first question, and number of functional categories, associated with our second question, among the three scenarios at the local scale, we first defined nine levels of extinction, from 10 to 90% of extinction, and computed the functional rarity and the number of remaining functional categories in the scenarios at each step of extinction.

Then, we conducted non-parametric paired Friedman tests at each step of extinction to test for differences in functional rarity (first question) and number of functional categories (second question) and further pairwise comparisons using post-hoc analysis whenever we found a statistically significant difference among the scenarios (Leitão et al. 2016). At the regional scale, we computed the 95% confidence interval of the null model and compared to the other two extinction scenarios (Leitão et al. 2016). In this way, if the pattern found in an extinction scenario falls out of this confidence interval, then we can assume a significant difference from the random expectation.

We adopted a significance level of 5%, and all analysis were performed in the R software (R Core Team 2020), using the packages vegan (Oksanen et al. 2019), funrar (Grenié et al. 2017), dplyr (Wickham et al. 2020), ade4 (Dray and Dufour 2007) and PMCMR (Pohlert 2014).

Results

We sampled 21,285 individuals of 95 species from 25 families and six orders (Appendix S1 – Table A1). The most abundant species were *Hyphessobrycon heterorhabdus* (Ulrey, 1894) (7,914 individuals), *Apistogramma regani* Kullander, 1980 (1,914 individuals) and *Microcharacidium weitzmani* Buckup, 1993 (1,797 individuals), which together accounted for > 50% of the sampling. Fourteen species had a local abundance of 1 and 28 species occurred in only one stream across the region (Appendix S1 – Table A1). At the local scale, species' scarcity index varied from 0.0001 to 0.993 (mean ± SD = 0.68 ± 0.30) and functional distinctiveness varied from 0.163 to 1 (0.48 ± 0.10). At the regional scale, the restrictiveness index varied from 0.079 to 0.984 (0.83 ± 0.23) and the functional uniqueness varied from 0 to 0.554 (0.093 ± 0.12). The four most tolerant species survived under 0 of habitat integrity, whereas the two most sensible species survived only under 6.72 of habitat integrity (2.95 ± 1.44) (Appendix S1 – Table A1).

The effects of extinction in the community's functional rarity differed depending on which set of species were extinct first. Once we extinct species based on their vulnerability to habitat integrity loss, the local functional distinctiveness increased in the scenario in which sensible species were extinct first, and decreased in the scenario in which tolerant species were extinct first (Fig. 2A). Both scenarios differed from each other and from the random extinction scenario at all nine levels of extinction at local scale. At the regional scale, we found the inverse pattern: in the extinction scenario of sensible species extinction, the regional uniqueness increased above the random expectation after 20% of extinction (Fig. 2B). Otherwise, in the scenario in which tolerant species were extinct first the regional uniqueness decreased below the random expectation after 25% species being extinct (Fig. 2B).

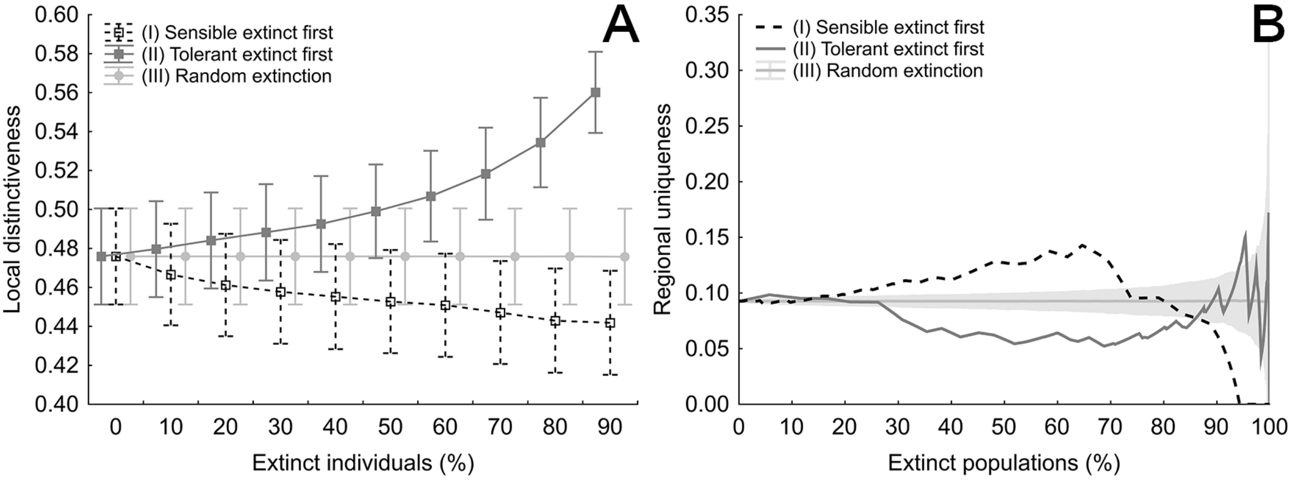

Figure 2. Relationship between mean functional rarity as distinctiveness at a local scale (A), and as uniqueness at a regional scale (B) in function of the extinction of individuals/populations in different extinction scenarios. Shapes in the middle are mean values of distinctiveness, and vertical bars are their 95% confidence intervals. The grey cloud around the regional random extinction scenario in B represents confidence intervals from the null model.

Regarding the patterns of functional extinction of the community at the local scale, in the scenario in which sensible species were extinct first, the first functional category was lost after <10% species being extinct (Fig. 3A). The first functional category lost after sensible species extinction varied across the streams. The piscivore functional category was lost first in 38.10% of the streams, followed by detritivore in 28.57% of the streams, algivore in 15.87%, hematophagous in 14.29%, and allochthonous and autochthonous invertivore, each in 1.59% of the streams. Otherwise, in the scenario in which tolerant species were extinct first, the first functional category was lost only after ~90% of extinction (Fig. 3A). The first functional category lost also varied across the streams. Algivore was lost first in 43.10% of the streams, followed by detritivores and allochthonous invertivore, each in 20.69% of the streams, hematophagous in 8.62%, and autochthonous invertivore and piscivore, each in 3.45% of the streams (Fig. 3A). Both scenarios of extinction were different from each other and the random expectation at all steps of extinction.

At the regional scale, the first functional category was lost at 10% of species being extinct in the scenario of sensible species extinction, whereas more than 95% of species were extinct in the scenario of tolerant species extinction to observe such loss of functions (Fig. 3B). When sensible species were extinct first, the region lost hematophagous fish first, at 10% of extinction, then, at 40% of extinction, detritivores fish were regionally lost, followed by piscivores at ~70% of extinction, algivores at 75% and, finally, autochthonous invertivores were lost at 95% of extinction (Fig. 3B). On the other hand, when tolerant species were extinct first, the first functional category lost was hematophagous, at 95% of extinction (Fig. 3B). The scenario of sensible species extinction was always below the random expectation after 10% of extinction (i.e., functions were lost earlier than expected at random), but the scenario of tolerant species extinction never differed from the random expectation (Fig. 3B).

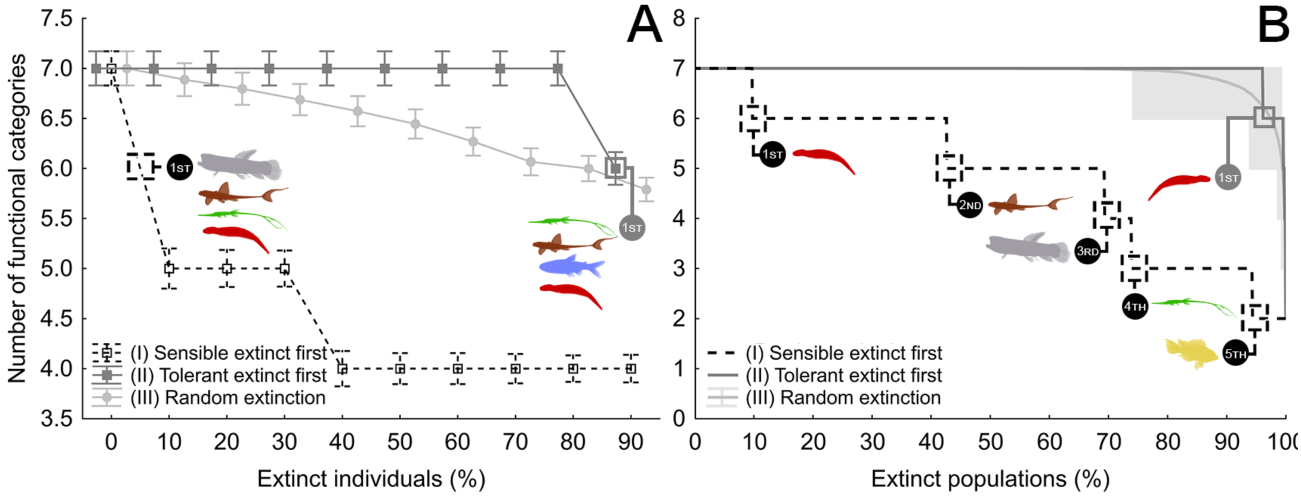

Figure 3. A plot of the number and first lost functional categories after extinction and at (A) local and (B) regional scale in the extinction scenarios. In the local plot (A), shapes in the middle are median values of the number of functions, and vertical bars are their confidence intervals. In the regional plot (B), the grey cloud around the random extinction scenario represents confidence intervals from the null model. Circles with 1st, 2nd, 3rd, 4th, and 5th represent the first, second, third, fourth and fifth lost functional category, respectively. Grey fish are piscivores, browns are detritivores, greens are algivores, reds are hematophagous, blue is allochthonous invertivore, and yellow is autochthonous invertivore.

Discussion

Our extinction scenarios driven by species' vulnerability to habitat loss revealed that vulnerable species, the ones that are rare and survive only under high habitat integrity, hold a distinct set of functional traits at local scale, partially corroborating our first hypothesis. Then, when these sensible species were locally extinct, the functional distinctiveness of the community decreased as only tolerant species remain in the community. These tolerant species contribute less to the local distinctiveness of streams, this is due to the fact that locally tolerant species frequently share its functional traits with other species in the same stream, a property known as functional redundancy (Biggs et al. 2020). This implies that when tolerant species are locally extinct, the ecosystem loses functional redundancy, which is associated with the resilience of the ecosystem. Nevertheless, sensible species are actually the most vulnerable to extinction after habitat loss, as shown by several studies thus far (e.g., Peressin et al. 2018, Zambrano et al. 2019, Dopheide et al. 2020, Edwards et al. 2020, Rocha-Santos et al. 2020). The extirpation of these sensible species will culminate in the disappearance of functions not provided by others in the community, bringing further disruption of important ecosystem processes that take place in Amazonian streams.

At the regional scale, tolerant species, the ones that are widespread across the basin and are able to survive under low habitat integrity, hold the unique functional traits contrary to our first hypothesis. This implies that sensible species, which hold distinct functional traits in each stream, actually hold redundant functional traits when we consider the entire region. The high uniqueness of the functional traits provided by tolerant species may assure the maintenance and resilience of these unique traits in the region, since these tolerant species are less prone to extinction due to habitat loss (Casatti et al. 2015b, Biggs et al. 2020). In this way, conservation programs and initiatives should choose to preserve a larger area, including entire basins in its delimitations to efficiently prevent functional loss of unique functions provided by streams fish, but unfortunately, this is not the reality of conservation programs in Brazil (Azevedo-Santos et al. 2019). Although the country has a national system that provides standard proceedings to implementing conservation units (Law 9985/2000: http://www.planalto.gov.br/ccivil_03/leis/l9985.htm), freshwater ecosystems are not the target of conservation in the majority of units, but rather terrestrial fauna and forests (Azevedo-Santos et al. 2019). Especially in the Amazon, the Brazilian government has an ongoing program that already covers 43% of the Amazon rainforest, but, as shown by Frederico et al. (2018), these conservation units fail to protect priority areas to stream fish.

Some studies also investigate the effects habitat loss in functional indexes, such as functional richness (Ibarra and Martin 2015), functional heterogeneity (García et al. 2013), and alpha and beta facets of functional diversity (Si et al. 2016, Brodie et al. 2021). Although the usage of functional indexes may reveal overall losses in ecosystem functioning, it fails at indicating which functional traits are at higher risk of extinction and the effects of its possible extinction to ecosystem functioning, an issue that ecological studies may overcome through investigating extinction patterns of individual functional traits (Zambrano et al. 2019). As we tracked the loss of individual functional categories of the fish diet trait to answer our second question, we found that, when sensible species were extinct, an abrupt loss of functional categories occurs right after the extinct of few individuals and populations at local and regional scales, respectively. Otherwise, when tolerant species were extinct, the loss of functional categories only started after many species were extinct. This pattern reveals how functional redundancy (i.e., how many species supports each functional category) is structured among these two distinct sets of species. Sensible species are often less redundant, given that few species distributed in few individuals/populations support distinct traits, thus, the extinction of these species should easily lead to functional extinctions in the ecosystem (Walker 2016, Biggs et al. 2020). On the other hand, tolerant species are often more redundant, given that many individuals/populations are supporting the same functional category, thus, their extinction is less prone to lead to functional extinctions in the ecosystem since even if a species is extinct, others will still provide the same function to ecosystem dynamics (Cadotte et al. 2011, Biggs et al. 2020).

The pervasive effects of habitat loss scale from community to affect ecosystem functioning. In marine ecosystems, for instance, habitat loss through grazing by urchins lowers net ecosystem production and ecosystem respiration (Edwards et al. 2020). In tropical Atlantic rainforests, habitat loss by deforestation negatively affects reproductive traits supported by sensible tree species (Rocha-Santos et al. 2020). Regarding stream ecosystem in Amazon, we should expect cascade effects in ecosystem functioning after the extinction of piscivores, detritivores, algivores and hematophagous, the most vulnerable functional categories found in our study.

Piscivores control the population of its prey, which are often invertivores fish (Gilliam et al. 1993, Greenberg et al. 2005, Lovell et al. 2017). Thus, when piscivores disappear, the abundance of invertivores fish may increases due to a lower predation pressure, what leads to increases in the predation pressure in invertebrates (Gilliam et al. 1993, Greenberg et al. 2005, Lovell et al. 2017). This allows an overgrowth of algae in streams, which are less grazed thanks to the low abundance of grazing invertebrates, leading to detrimental effects on water quality and oxygen availability (Greenberg et al. 2005), but this inference is yet to be experimentally tested for the neotropics. The extinction of algivore fish will also lead to algae overgrowth in streams due to the reduction in grazing pressure, resulting in similar effects to ecosystem functioning as the extinction of piscivores (Power et al. 1988, Flecker et al. 2002). Nonetheless, we should expect algae overgrowth in tropical streams after habitat loss, especially under loss of riparian vegetation due deforestation (Fugère et al. 2018). After deforestation in the margins, canopy density decreases, what increase solar radiation in the stream, further allowing algae to grow due to higher resource availability (Bixby et al. 2009, Fugère et al. 2018). Thus, habitat loss combined with extinction of piscivores and algivores will likely trigger a eutrophication process in Amazonian streams, creating a hypoxic system with low visibility and water quality (Flecker et al. 2002).

Hematophagous stream fish from the Trichomycteridae family indirectly lead to reductions in intraspecific competition among its host since it controls host' abundance (Spotte 2002). Only *Ituglanis* sp. and *Paracanthopoma* sp. support this functional category in the ecosystem, they make an incision in its host gills to engorge themselves in blood, leaving its host vulnerable to diseases andindirectly leading to host' death (Zuanon and Sazima 2004). Specifically, *Paracanthopoma* sp. uses its host to migrate between different habitat, contributing to nutrient exchange between different streams and rivers (Zuanon and Sazima 2005). Due to the lack of redundancy, hematophagous are at higher risk of extinction. If these species disappear, we may expect increases in host' abundance and associated increases in intraspecific competition among hosts, beyond the loss of a pathway of nutrient intake into streams (Zuanon and Sazima 2004, 2005).

Detritivore fish take part in the nutrient cycle of the streams as it feeds of the organic matter accumulated at stream bottom, releasing nutrients such as organic carbon, nitrogen and phosphorus into the stream, which are carried downriver by water flow (Flecker 1996, Taylor et al. 2006). This functional category was frequently one of the most vulnerable to extinction, and if these species disappear, then we can expect a disruption in nutrient cycling in the stream where organic matter will accumulate in stream's bottom and important nutrients will not be released into the water nor carried downriver (Taylor et al. 2006). Although this higher risk of extinction found in our study, there is evidence that some species of detritivore fish actually increases in abundance after deforestation and habitat loss, especially fish who play a role as detritivore-algivore in the ecosystem (Casatti et al. 2012, Peressin et al. 2018, Reis et al. 2020). After habitat loss, algae and organic matter are abundant in streams (Fugère et al. 2018), what allows for detritivore-algivore fish to grow in abundance (Casatti et al. 2012). However, this assumption is only true if these detritivore fish are tolerant enough to survive under the environmental conditions established after habitat loss, which is not always the case since some detritivore species are highly exigent regarding the nutritional quality of its food (Fugi and Hahn 1991).

Habitat loss is the main human modification driving the ongoing sixth mass extinction, in which species are disappearing a thousand times faster than expected (Pimm et al. 2014). At Amazon, deforestation rates only increase due to land use activities, threatening rare (Leitão et al. 2016, De Oliveira et al. 2018) and non-tolerant species (McKinney and Lockwood 1999, Michalski et al. 2007), which are prone to extinction during the Anthropocene. Throughout our realistic scenarios of extinction, which spatially scale the extirpation of individuals as species are extinct based on an integration of its rarity and vulnerability to habitat loss, we highlight that if these rare and non-tolerant (sensible species) fish indeed are extirpated from Amazon streams, we should expect abrupt functional losses at local scale, further altering ecosystem functioning. If the ongoing mass extinction event driven by habitat loss indeed targets sensible species to extinction, then the Amazon stream ecosystem will likely change after the extinction of detritivores, piscivores, algivores and hematophagous fish. The extinction of these functional categories will likely trigger a eutrophication process in the streams, beyond interrupt nutrient cycling of important nutrients to ecosystem maintenance. A way to mitigate these negative effects may be through the implementation of conservation units that comprise entire basins in its delimitation.

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Supporting information

Appendix A: Taxonomic composition, total abundance, occurrence, diet trait and its respectively functional categories, minimal integrity needed for species to survive, and local and regional indexes of the taxonomic and functional rarity and vulnerability to habitat loss.

Table A1. Taxonomic composition, total abundance (TAb), occurrence (Occ; as the number of streams that the species occurred within the 63 sampled), the proportion of each functional category in the diet functional trait for species, minimal integrity needed for species to survive (MiInt), and local and regional indexes of the taxonomic and functional rarity and vulnerability to habitat loss of the fish assemblage in the 63 sampled streams. AuI = Autochthonous Invertivore; AlI = Allochthonous Invertivore; Pis = Piscivores; Alg = Algivore; Det = Detritivore; Lrv = Larvivorous; Hmt = Hematophagous; LcSc = Local Scarcity; RgRst = Regional Restrictiveness; LcDst = Local Distinctiveness; RgUni = Regional Uniqueness; Lc = Local; Rg = Regional.

Taxon	TAb	Occ	Diet fuzzy trait							MiInt	Tax. rarity		Func. rarity		Vuln. to habitat loss	
			AuI	AlI	Pis	Alg	Det	Lrv	Hmt		LcSc	RgRst	LcDst	RgUni	Lc	Rg
BELONIFORMES																
Belonidae																
Potamorrhaphis eigenmanni Miranda Ribeiro, 1915	1	1	0.08	0.77	0.15	0.00	0.00	0.00	0.00	0.01	0.97	0.98	0.83	0.14	0.49	0.50
CHARACIFORMES																
Characidae																
Astyanax bimaculatus (Linnaeus, 1758)	12	1	0.03	0.70	0.06	0.00	0.00	0.20	0.00	0.21	0.72	0.98	0.40	0.15	0.47	0.60
Bario steindachneri (Eigenmann, 1893)	3	3	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.30	0.96	0.95	0.71	0.01	0.63	0.63
Hemigrammus belottii (Steindachner, 1882)	331	18	0.00	0.98	0.00	0.00	0.00	0.02	0.00	0.33	0.57	0.71	0.72	0.01	0.45	0.52
Hemigrammus geisleri Zarske & Géry, 2007	1	1	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.22	0.97	0.98	0.40	0.00	0.59	0.60
Hemigrammus ocellifer (Steindachner, 1882)	187	17	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.49	0.70	0.73	0.39	0.00	0.60	0.61
Hemigrammus rhodostomus Ahl, 1924	1	1	0.45	0.00	0.09	0.46	0.00	0.00	0.00	0.00	0.95	0.98	0.87	0.10	0.47	0.49

Hemigrammus rodwayi Durbin, 1909	508	5	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.14	0.31	0.92	0.47	0.00	0.22	0.53
Hemigrammus sp.	86	1	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.01	0.06	0.98	0.73	0.00	0.04	0.50
Hemigrammus unilineatus (Gill, 1858)	55	2	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.17	0.24	0.97	0.34	0.00	0.21	0.57
Hyphessobrycon bentosi Durbin, 1908	3	3	0.25	0.25	0.00	0.00	0.00	0.50	0.00	0.09	0.95	0.95	0.44	0.12	0.52	0.52
Hyphessobrycon heterorhabdus (Ulrey, 1894)	7914	56	0.13	0.38	0.00	0.00	0.00	0.50	0.00	0.22	0.22	0.11	0.39	0.15	0.22	0.16
Knodus victoriae (Steindachner, 1907)	8	2	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.50	0.68	0.97	0.50	0.00	0.59	0.73
Moenkhausia collettii (Steindachner, 1882)	3	3	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.17	0.92	0.95	0.38	0.00	0.55	0.56
Moenkhausia comma Eigenmann, 1908	10	4	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.23	0.92	0.94	0.37	0.00	0.58	0.58
Moenkhausia oligolepis (Günther, 1864)	14	6	0.16	0.48	0.06	0.05	0.01	0.24	0.00	0.22	0.95	0.90	0.38	0.23	0.58	0.56
Phenacogaster pectinatus (Cope, 1870)	1	1	0.29	0.38	0.00	0.03	0.01	0.29	0.00	0.50	0.87	0.98	0.49	0.10	0.68	0.74
Serrapinnus sp.	3	1	0.72	0.17	0.01	0.10	0.00	0.00	0.00	0.21	0.92	0.98	0.87	0.07	0.57	0.60
Crenuchidae																
Characidium etheostoma Cope, 1872	65	14	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.85	0.78	0.79	0.00	0.62	0.59
Characidium sp.	4	1	0.60	0.03	0.00	0.03	0.00	0.34	0.00	0.30	0.69	0.98	0.59	0.09	0.50	0.64
Characidium zebra Eigenmann, 1909	1	1	0.42	0.01	0.01	0.00	0.00	0.56	0.00	0.50	0.87	0.98	0.63	0.08	0.68	0.74
Crenuchus spilurus Günther, 1863	150	12	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.33	0.78	0.81	0.38	0.00	0.56	0.57
Melanocharacidium dispilomma Buckup, 1993	2	2	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.22	0.92	0.97	0.54	0.00	0.57	0.59
Microcharacidium weitzmani Buckup, 1993	1797	35	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.36	0.43	0.44	0.49	0.00	0.40	0.40
Curimatidae																
Curimatopsis crypticus Vari, 1982	18	3	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.09	0.88	0.95	1.00	0.00	0.49	0.52
Steindachnerina amazonica (Steindachner, 1911)	1	1	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.21	0.97	0.98	0.99	0.54	0.59	0.60
Erythrinidae																
Erythrinus erythrinus (Bloch & Schneider, 1801)	537	47	0.17	0.33	0.33	0.00	0.00	0.17	0.00	0.47	0.72	0.25	0.61	0.23	0.60	0.36
Hoplias curupira Oyakawa & Mattox, 2009	2	1	0.25	0.25	0.25	0.00	0.00	0.25	0.00	0.38	0.94	0.98	0.48	0.00	0.66	0.68
Hoplias malabaricus (Bloch, 1794)	54	22	0.31	0.00	0.69	0.00	0.00	0.00	0.00	0.22	0.88	0.65	0.91	0.02	0.55	0.43
Gasteropelecidae																
Carnegiella strigata (Günther, 1864)	67	7	0.10	0.90	0.00	0.00	0.00	0.00	0.00	0.25	0.66	0.89	0.73	0.08	0.46	0.57
Iguanodectidae																
Bryconops caudomaculatus (Günther, 1864)	7	2	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.00	0.86	0.97	0.26	0.00	0.43	0.48
Bryconops sp.	26	4	0.00	0.67	0.00	0.00	0.00	0.33	0.00	0.10	0.85	0.94	0.38	0.13	0.48	0.52
Iguanodectes rachovii Regan, 1912	1086	36	0.00	0.50	0.00	0.17	0.00	0.33	0.00	0.37	0.40	0.43	0.51	0.19	0.38	0.40

Lebiasinidae																
Copella arnoldi (Regan, 1912)	851	25	0.15	0.35	0.00	0.10	0.00	0.40	0.00	0.44	0.39	0.60	0.35	0.15	0.41	0.52
Nannostomus beckfordi Günther, 1872	11	1	0.50	0.00	0.00	0.50	0.00	0.00	0.00	0.21	0.74	0.98	0.97	0.00	0.48	0.60
Nannostomus nitidus Weitzman, 1978	103	5	0.50	0.00	0.00	0.50	0.00	0.00	0.00	0.06	0.58	0.92	0.93	0.00	0.32	0.49
Nannostomus trifasciatus Steindachner, 1876	117	21	0.33	0.00	0.00	0.33	0.00	0.33	0.00	0.36	0.79	0.67	0.63	0.00	0.58	0.51
Pyrrhulina brevis Steindachner, 1876	1239	58	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.23	0.62	0.08	0.38	0.00	0.43	0.15
CICHLIFORMES																
Cichlidae																
Aequidens tetramerus (Heckel, 1840)	312	46	0.00	0.40	0.00	0.40	0.00	0.20	0.00	0.27	0.81	0.27	0.64	0.33	0.54	0.27
Apistogramma agassizii (Steindachner, 1875)	221	12	0.22	0.22	0.00	0.11	0.00	0.44	0.00	0.37	0.64	0.81	0.32	0.14	0.50	0.59
Apistogramma regani Kullander, 1980	1914	53	0.33	0.22	0.00	0.00	0.00	0.44	0.00	0.30	0.39	0.16	0.41	0.09	0.34	0.23
Crenicichla reticulata (Heckel, 1840)	4	3	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.23	0.94	0.95	0.86	0.00	0.59	0.59
Crenicichla saxatilis (Linnaeus, 1758)	158	28	0.33	0.00	0.33	0.00	0.00	0.33	0.00	0.22	0.78	0.56	0.66	0.00	0.50	0.39
Heros sp.	1	1	0.25	0.25	0.00	0.00	0.25	0.25	0.00	0.00	0.95	0.98	0.57	0.00	0.47	0.49
Nannacara taenia Regan, 1912	213	14	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.37	0.62	0.78	0.39	0.00	0.49	0.57
Satanoperca jurupari (Heckel, 1840)	8	2	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.97	0.90	0.00	0.44	0.48
CYPRINODONTIFORMES																
Poeciliidae																
Poecilia sp.	51	1	0.28	0.27	0.00	0.00	0.14	0.31	0.00	0.17	0.03	0.98	0.35	0.18	0.10	0.58
Rivulidae																
Anablepsoides sp.	1	1	0.15	0.26	0.14	0.13	0.13	0.20	0.00	0.25	0.95	0.98	0.54	0.34	0.60	0.62
Anablepsoides urophthalmus (Günther, 1866)	493	44	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.14	0.74	0.30	0.56	0.15	0.44	0.22
Laimosemion strigatus (Regan, 1912)	245	8	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.38	0.35	0.87	0.46	0.00	0.36	0.62
GYMNOTIFORMES																
Gymnotidae																
Gymnotus carapo Linnaeus, 1758	10	8	0.55	0.04	0.00	0.00	0.07	0.33	0.00	0.31	0.95	0.87	0.59	0.09	0.63	0.59
Gymnotus coropinae Hoedeman, 1962	229	39	0.50	0.00	0.25	0.00	0.00	0.25	0.00	0.46	0.79	0.38	0.66	0.16	0.63	0.42
Gymnotus pantherinus (Steindachner, 1908)	115	24	0.49	0.11	0.21	0.02	0.00	0.17	0.00	0.40	0.79	0.62	0.64	0.16	0.60	0.51
Gymnotus sp.	7	6	0.33	0.00	0.33	0.00	0.00	0.33	0.00	0.36	0.93	0.90	0.61	0.00	0.65	0.63
Hypopomidae																
Brachyhypopomus beebei (Schultz, 1944)	77	10	0.20	0.00	0.00	0.00	0.00	0.80	0.00	0.49	0.89	0.84	0.46	0.00	0.69	0.67

Brachyhypopomus brevirostris (Steindachner, 1868)	55	16	0.20	0.00	0.00	0.00	0.00	0.80	0.00	0.44	0.88	0.75	0.45	0.00	0.66	0.59
Brachyhypopomus sp.1	19	3	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.23	0.81	0.95	0.35	0.00	0.52	0.59
Brachyhypopomus sp.2	235	24	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.37	0.80	0.62	0.45	0.00	0.59	0.49
Brachyhypopomus sp.3	12	6	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.37	0.93	0.90	0.40	0.00	0.65	0.64
Brachyhypopomus sp.4	7	3	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.40	0.88	0.95	0.35	0.00	0.64	0.68
Hypopygus lepturus Hoedeman, 1962	78	14	0.40	0.20	0.00	0.00	0.00	0.40	0.00	0.25	0.83	0.78	0.42	0.09	0.54	0.51
Microsternarchus bilineatus Fernández-Yépez, 1968	69	12	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.29	0.79	0.81	0.40	0.00	0.54	0.55
Rhamphichthyidae																
Gymnorhamphichthys petiti Géry & Vu, 1964	442	29	0.87	0.00	0.00	0.00	0.00	0.13	0.00	0.29	0.55	0.54	0.78	0.10	0.42	0.41
Sternopygidae																
Eigenmannia sp.	1	1	0.33	0.00	0.00	0.00	0.33	0.33	0.00	0.48	0.96	0.98	0.57	0.00	0.72	0.73
Eigenmannia trilineata López & Castello, 1966	2	1	0.00	0.00	0.00	0.00	0.18	0.82	0.00	0.17	0.87	0.98	0.60	0.15	0.52	0.58
Sternopygus macrurus (Bloch & Schneider, 1801)	2	2	0.45	0.00	0.00	0.00	0.05	0.50	0.00	0.30	0.94	0.97	0.57	0.06	0.62	0.64
SILURIFORMES																
Aspredinidae																
Bunocephalus coracoideus (Cope, 1874)	7	2	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.17	0.81	0.97	0.43	0.00	0.49	0.57
Auchenipteridae																
Tetranematichthys wallacei Vari & Ferraris, 2006	1	1	0.25	0.25	0.25	0.00	0.00	0.25	0.00	0.49	0.96	0.98	0.53	0.00	0.73	0.74
Callichthyidae																
Callichthys (Linnaeus, 1758)	6	5	0.33	0.00	0.00	0.00	0.33	0.33	0.00	0.53	0.98	0.92	0.65	0.00	0.75	0.72
Corydoras melanistius Regan, 1912	3	1	0.25	0.25	0.00	0.00	0.25	0.25	0.00	0.50	0.66	0.98	0.60	0.00	0.58	0.74
Corydoras sp.	5	1	0.26	0.00	0.00	0.50	0.00	0.24	0.00	0.17	0.70	0.98	0.71	0.24	0.44	0.58
Megalechis picta (Müller & Troschel, 1849)	1	1	0.80	0.10	0.00	0.10	0.00	0.00	0.00	0.49	0.96	0.98	0.74	0.07	0.73	0.74
Megalechis thoracata (Valenciennes, 1840)	2	2	0.25	0.00	0.00	0.00	0.25	0.50	0.00	0.67	0.97	0.97	0.48	0.24	0.82	0.82
Cetopsidae																
Denticetopsis epa Vari, Ferraris & de Pinna, 2005	14	9	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.39	0.90	0.86	0.64	0.00	0.65	0.63
Denticetopsis sp.	1	1	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.17	0.87	0.98	0.67	0.00	0.52	0.58
Helogenes marmoratus Günther, 1863	510	54	0.00	0.57	0.00	0.00	0.00	0.43	0.00	0.20	0.70	0.14	0.43	0.10	0.45	0.17
Doradidae																
Acanthodoras cataphractus (Linnaeus, 1758)	1	1	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.67	0.97	0.98	0.86	0.00	0.82	0.83
Heptapteridae																

Gladioglanis conquistador Lundberg et al. 1991	39	2	0.00	0.33	0.00	0.00	0.00	0.67	0.00	0.41	0.56	0.97	0.44	0.19	0.49	0.69
Mastiglanis asopos Bockmann, 1994	29	6	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.31	0.82	0.90	0.49	0.00	0.57	0.61
Pimelodella geryi Hoedeman, 1961	2	1	0.24	0.00	0.52	0.00	0.00	0.24	0.00	0.25	0.91	0.98	0.74	0.26	0.58	0.62
Pimelodella sp.	8	6	0.30	0.02	0.68	0.00	0.00	0.00	0.00	0.22	0.94	0.90	0.90	0.02	0.58	0.56
Rhamdia muelleri (Günther, 1864)	12	5	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.47	0.89	0.92	0.96	0.29	0.68	0.70
Rhamdia quelen (Quoy & Gaimard, 1824)	3	1	0.35	0.09	0.45	0.03	0.04	0.04	0.00	0.25	0.87	0.98	0.79	0.16	0.56	0.62
Rhamdia sp.	2	2	0.42	0.00	0.25	0.25	0.00	0.08	0.00	0.41	0.97	0.97	0.75	0.31	0.69	0.69
Loricariidae																
Farlowella amazonum (Günther, 1864)	21	9	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.33	0.84	0.86	0.96	0.00	0.58	0.59
Otocinclus mura Schaefer, 1997	4	1	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.41	0.87	0.98	0.98	0.00	0.64	0.70
Rineloricaria hasemani Isbrücker & Nijssen, 1979	3	2	0.33	0.00	0.00	0.33	0.00	0.33	0.00	0.30	0.93	0.97	0.61	0.00	0.62	0.64
Rineloricaria sp.	2	2	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.17	0.90	0.97	0.97	0.00	0.54	0.57
Pseudopimelodidae																
Batrochoglanis raninus (Valenciennes, 1840)	6	4	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.31	0.88	0.94	0.78	0.00	0.59	0.62
Microglanis poecilus Eigenmann, 1912	1	1	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.25	0.95	0.98	0.42	0.00	0.60	0.62
Trichomycteridae																
Ituglanis amazonicus (Steindachner, 1882)	113	24	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.31	0.81	0.62	0.40	0.00	0.56	0.46
Ituglanis sp.	19	5	0.25	0.00	0.25	0.00	0.00	0.25	0.25	0.31	0.83	0.92	0.69	0.37	0.57	0.62
Paracanthopoma sp.	25	7	0.00	0.00	0.00	0.00	0.00	0.40	0.60	0.44	0.84	0.89	0.82	0.55	0.64	0.66
Potamoglanis hasemani (Eigenmann, 1914)	183	20	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.38	0.74	0.68	0.50	0.00	0.56	0.53
SYNBRANCHIFORMES																
Synbranchidae																
Synbranchus marmoratus Bloch, 1795	2	1	0.19	0.10	0.19	0.00	0.00	0.52	0.00	0.25	0.91	0.98	0.43	0.27	0.58	0.62

CONCLUSÃO GERAL

Evidenciamos que espécies raras, em escala local e regional, e sensíveis à perda de habitat, em escala local, são as espécies de peixes que desempenham papéis mais distintos no funcionamento dos ecossistemas de riachos amazônicos. Entretanto, em escala regional, espécies de peixes tolerantes à perda de habitat são as que desempenham papéis únicos no funcionamento do ecossistema, o que pode assegurar a resiliência dos riachos na região amazônica. Os cenários de extinção simulados nos dois capítulos indicaram que os riachos sofrerão uma perda funcional abrupta logo após a extinção de poucas espécies raras e sensíveis à perda de habitat em escala local e regional. Em contrapartida, espécies comuns e tolerantes suportam a extinção de muitos indivíduos até que alguma perda funcional ocorra no ecossistema, o que garante a resiliência das funções que eles desempenham. Se o atual evento de extinção em massa promovido pela perda de habitat realmente levar à extinção de espécies raras e sensíveis, como indicado por diversos estudos (e.g., BUENO *et al.*, 2018; KIESSLING; ABERHAN, 2007; LYONS *et al.*, 2005; MOUILLOT *et al.*, 2013; SYKES *et al.*, 2020), então podemos esperar após a extinção de peixes detritívoros, piscívoros, algívoros e hematófagos. Estas extinções funcionais podem desencadear um processo de eutrofização nos riachos, além de interromper a ciclagem de nutrientes importantes para a manutenção do ecossistema. Alertamos para a urgência de se conservar áreas prioritárias para peixes de riacho, preferencialmente incluindo bacias hidrográficas inteiras em suas delimitações para assegurar o funcionamento da região. Considerando a rápida extinção de espécies no Antropoceno, uma abordagem baseada em identificar quais funções são mais vulneráveis à extinção pode agregar à clássica identificação de espécies vulneráveis e prover *insights* acerca de como o funcionamento do ecossistema pode mudar em consequência de futuras extinções de espécies.

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