



HAL
open science

FUNCTIONAL STRUCTURE AND CONSERVATION OF STREAM FISH ASSEMBLAGES IN THE BRASILIAN AMAZON

Rafael Pereira Leitao

► **To cite this version:**

Rafael Pereira Leitao. FUNCTIONAL STRUCTURE AND CONSERVATION OF STREAM FISH ASSEMBLAGES IN THE BRASILIAN AMAZON. Ecosystems. Université Montpellier; Instituto nacional de pesquisas da Amazônia (Brésil), 2015. English. NNT : 2015MONT293 . tel-03222089

HAL Id: tel-03222089

<https://theses.hal.science/tel-03222089v1>

Submitted on 10 May 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

THÈSE

Pour obtenir le grade de
Docteur

Délivré par UNIVERSITÉ MONTPELLIER

**Préparée au sein de l'école doctorale SIBAGHE
Et de l'unité de recherche ECOSYM/MARBEC**

Spécialité : Ecosystèmes et sciences agronomiques

Présentée par RAFAEL PEREIRA LEITÃO

**LA STRUCTURE FONCTIONNELLE ET LA
CONSERVATION DES COMMUNAUTÉS DE
POISSONS DES RUISSEAUX EN AMAZONIE**

Soutenue le 27 Mars 2015 devant le jury composé de

M. David MOUILLOT, Professeur,
Université Montpellier

Directeur de thèse

M. Thierry OBERDORFF, Senior Scientist,
Institut de Recherche pour le Développement

Rapporteur

M. Fabricio Barreto TERESA, Professeur,
Universidade Estadual de Goiás, Brésil

Rapporteur

M. Bruce Rider FORSBERG, Senior Scientist,
Instituto Nacional de Pesquisas da Amazônia

Président du Jury/
Examineur



Thèse en cotutelle



Instituto Nacional de Pesquisas da Amazônia
Programa de Pós-Graduação em Biologia de
Água Doce e Pesca Interior
Brazil



Université Montpellier
Ecosystèmes & Sciences Agronomiques
France

**FUNCTIONAL STRUCTURE AND CONSERVATION OF STREAM FISH
ASSEMBLAGES IN THE BRAZILIAN AMAZON**

RAFAEL PEREIRA LEITÃO

Supervisors:

Dr. JANSEN A. S. ZUANON
Instituto Nacional de Pesquisas da Amazônia

Dr. DAVID MOUILLOT
Université Montpellier

Thesis presented in co-supervision to obtain the PhD degree in Biological Sciences, doctoral specialist in: “Biologia de Água Doce e Pesca Interior (Instituto Nacional de Pesquisas da Amazônia)”, and “Ecosystèmes & Sciences Agronomiques (Université Montpellier)”.

Manaus, Amazonas

March 2015

*Dedico este trabalho à Dani,
pelo amor e companheirismo
ao longo de toda esta jornada,
aos meus pais, pelo carinho
e apoio incondicional,
e à minha querida
tia Lúcia (in memoriam),
por ter me ensinado como
a vida deve ser simples e plena.*

ACKNOWLEDGEMENTS

Trabalhar na Amazônia é definitivamente um privilégio e, acima de tudo, um enorme desafio! Lembro exatamente do pensamento que tive ao sobrevoar pela primeira vez a Grande Floresta: “Como alguém pode conseguir entender o que se passa ali embaixo?”. Depois de alguns anos, ainda penso nisso... Estamos longe, muito longe mesmo, de conseguir desvendar toda essa riqueza maravilhosa de formas de vida... Este é certamente o meu maior estímulo e, provavelmente, da maioria dos pesquisadores que já passaram ou ainda estão por aqui... E uma coisa é muito certa: é impossível entender a Amazônia sozinho...

Agradeço imensamente ao meu orientador e amigo, Jansen Zuanon, pelo estímulo constante ao meu crescimento como biólogo, naturalista, pesquisador e, acima de tudo, como pessoa. Obrigado pela oportunidade de trabalhar num lugar tão fantástico, pelo ensinamento irrestrito sobre a história natural dos peixes e sobre a ecologia da Amazônia, pelos *insights* para montar “quebra-cabeças” que parecem impossíveis de serem solucionados, e pelos longos e inspiradores papos regados a um bom vinho. Quem já teve a oportunidade, sabe o quão prazeroso e gratificante é trabalhar e conviver com uma pessoa tão especial! Valeu merrrrrrmo! Você é DFJ!!!

Je voudrais remercier à David Mouillot pour le stimulus à réfléchir sur les grandes questions écologiques et rechercher les “lacunes”, et pour l’accessibilité et la patience de superviser à un étudiant statistiquement très limitée. Finalement, je vous remercie, mon garant :), pour toute l’aide à mon merveilleux séjour à Montpellier.

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes), e ao Programa de Doutorado Sanduíche no Exterior (PDSE) pelo auxílio financeiro.

Ao Instituto Nacional de Pesquisas da Amazônia (INPA) e ao Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior (BADPI), em especial à Sidineia Amadio, à Angela Varela, e à Carminha, não só por todo o auxílio administrativo, mas principalmente pela convivência agradável e leve, marca reconhecida da “família BADPI”.

À amiga e conselheira Érica Caramaschi, pelo apoio de sempre, principalmente quando me deu muita força para trilhar novos caminhos.

Ao Jorgito Botero e à Dani Garcez, os maiores incentivadores para que eu conhecesse a Amazônia e estudasse no INPA! A dica foi perfeita!

Aos integrantes do Projeto Igarapés (e associados rsrs)! Em especial, aos grandes amigos: Zé “Julin” e sua linda e “crescente” família (Laurinha, Teteu & Clara); Akemi “Japashow” (a manauara/japa mais fajuta que tive a alegria de conhecer); Heldão e seu carron & violão, parceirasso do início ao fim dessa jornada; Titica (o churrasqueiro mais nerd e gente fina de Manaus!) & sua querida Cris; Gi Vilara, Marcelão & Gabi (gastronomia de altíssima qualidade e diversão certa de vários fins de semana!); Galuch (parceiro de sala e daquela gelada “de leve” de sexta!). À Renas e Maeda, pela primeira acolhida na salinha! À Lucélia e Fefo, por todo o incentivo à migração para Manaus e à entrada no projeto! Ao Izaias Xoumano, Thiago Dogão, Marlinha, Gabriel Mandrake, Gabi Cardoso, Fiote, Suzanne, Paulinha, Claudia, Jefito, Fabíola... Tenho muito orgulho de fazer parte dessa turma sensacional dos “pé moiado”!!!

À Rede Amazônia Sustentável (RAS), em especial ao amigo Toby Gardner, um dos maiores exemplos de como ser um líder! Mesmo com tantos obstáculos, sempre manteve um humor contagiante, gentileza e amabilidade com todos os integrantes (e são muitos!) desse projeto tão ambicioso! À Ciça Gontijo Leal, mineirinha grande parceira e figura essencial na construção desse trabalho... uma nova e grande amizade que tive o prazer de fazer nos últimos anos. Valeu demais por tantos e tantos helps, trocas de ideias, e ótimas gargalhadas... e também pelo queijun da Serra da Canastra, ô trem bão sô!!! Ao Bob Hughes, pela orientação, estímulo e incrível disposição nos trabalhos de campo (só mesmo um poraquê de quase 2 metros para conseguir tirá-lo do igarapé!). Ao Paulo Pompeu e Jos Barlow, pelas inúmeras ideias e divertidíssima convivência! Aos demais integrantes da equipe aquática da RAS: Débora Carvalho, Dougs, Túlião, Sussu, Leandro Juen, Karina, Vivian, Janaína, Zé Max, Ceceo, Miriam, Marcão, Leandro Brasil, Lucas, Lenise, Joana! Foram ótimos meses! A toda equipe do acampamento da LBA (Louro e cia; Santarém) e de Paragominas, por facilitar demais nossas longas estadias.

Aos diversos auxiliares de campo que tive o grande prazer de conviver nos mais diferentes e remotos lugares da Amazônia (Jããão, Nego, Elbin, Graveto, Matines, Pita, Valderi e muitos outros). Muito obrigado pela grande disposição em encarar as “quiçaças”, jararacas, e cabas, por sempre me acolherem tão bem em suas casas e em suas famílias... e, principalmente, muito obrigado por me passar o conhecimento genuíno. Aprendi e aprendo muito com vocês!

Ao Douglas Bastos, Fernando Mendonça, Fernando Cabeceira, Lucélia Carvalho e Raimundo Nonato Júnior, pela disponibilização de diversos pontos de amostragem que compõem o banco de dados utilizado na tese.

Ao Bruce Forsberg, João Rocha, Bruno Lima, Diego Souza, Sewbert Jati, João “Minhoca” Amaral, Pedro Barbosa, e demais integrantes do Laboratório de Ecossistemas Aquáticos do INPA, por todo o apoio nas coletas do Rio Negro!

Ao Sérgio Cunha e à Natasha Rabelo, pela imensa ajuda nas medidas ecomorfológicas dos peixes; e à Euri, Cris, e Fabíola, pelas análises de conteúdo estomacal.

Aos revisores do plano inicial de doutorado, do projeto sanduíche, e/ou da qualificação: Ana Petry, Claudia de Deus, Eduardo Venticinque, Fernando Pelicice, Gislene Vilara, Lilian Casatti, Paulo Bobrowiec e Pedro Peres-Neto. Muito obrigado pela atenção e pelo tempo investido para a melhora do trabalho. Suas sugestões foram muito bem vindas!

À Mariana Bender, pelas inúmeras e preciosas dicas sobre o processo de cotutela, e à Joana Nogueira, pela enorme ajuda com a papelada da UM2 nos últimos meses!

Ao André Dias, pelas sugestões e discussões sobre as análises do capítulo 1.

Ao LabSid, o laboratório mais aconchegante do INPA! Pra “aliviar a pressão” e sair da frente do computador, nada melhor do que muito peixe do Catalão na bancada e um cafezinho com prosa com essa moçada. Valeu demais: Seu Raimundo, Euri, Sérgio, Camilinha, Naty, Thatyla, Dani(s)! Não é possível falar do LabSid sem lembrar do nosso querido e iluminado Rodriguinho (você faz muita falta, cara... mas quem teve o privilégio de conviver contigo, mesmo que por um tempo muito menor do que gostaríamos, sabe que você continua alegrando a todos, onde quer que esteja...). Aos amigos da coleção de peixes! Pelo help no

campo, na identificação e no tombamento dos bichos... mas, principalmente, pela diversão que é visitar o lab mais louco e a “salinha mais xx” (apesar de certos xy intrusos) do INPA! Lucia, Madoka, Rafa e Burns, Batatinha, Rona, Bel, Dougs, Rovis, Marcelo, Clebinho, Belaco, Frank, Ximba e demais integrantes da famosa “mesa redonda”. Valeu demais, galera!

À l'équipe de SIBAGHE (UM2) e de Laratoire de Ecologie des Systèmes Marins Cotiers (ECOSYM/ UM2)! À Arthur Escalas, Charlotte Sirot, Claire Jacquet, David McKenzie, Fabien Leprieur, Jacques Panfili, Jennifer Tournois, Joelle Lopez, Monique Matignon-Boujot, Nicole Colin, Solange Fournier, Stéphanie D'Agata. J'ai appris beaucoup sur la culture de votre merveilleux pays avec vous! À Valeriano Parravicini, pour l'aide en “R”. À François Guilhaumon, merci pour toute l'aide en “R” et, principalement, pour le séjour dans votre maison et pour l'enseignement sur les Français. Un remerciement spécial à Sébastien Villéger, qui était un véritable co-directeur de thèse. Merci, Seb!

Ao Henrique “cachaça”, Lu Fidelis, e Braulio, pela acolhida antes e no início da migração pra Manaus! Ao Phil Mille, Gabi, Leo e Nina, pela acolhida e apoio na França!

Sair da nossa cidade natal, da nossa zona de conforto, e ficar distante da família e dos amigos de infância não é fácil. Mas tenho certeza de que, apesar de tanta saudade e tanta distância, sempre estivemos muito perto. Pelo amor, apoio, e força de sempre, agradeço aos meus amados pais, Matinho e Mércia! Ao Thiti & Di, Dani & Gi, Nathalia, Dudinha, Julinha(s), Bruninho, Breninho, Pedrinho, Lúcia (*in memoriam*), Jansen (*in memoriam*), Meco & Ge, Kaka & André, Tina & Marlon, Bea e toda querida família Redeker, Marli & Claudio, Álvaro, Denise, Dani & Zaza, Estela, Pedrunga, Elenita, Vitão, Ka, Melin, Mi, Lulu... Vocês tornam tudo muito mais fácil e divertido!

À Dani, que fez o seu “segundo doutorado”, estando sempre ao meu lado... pelo companheirismo, diversão, amor, carinho, e paz...

Esta é a contribuição #39 da série de publicações da Rede Amazônia Sustentável.

ABSTRACT

FUNCTIONAL STRUCTURE AND CONSERVATION OF STREAM FISH ASSEMBLAGES IN THE BRAZILIAN AMAZON

All ecosystems on Earth are facing unprecedented levels of human-induced disturbances. Tropical forests, which support enormous diversity of species, currently suffer the most dramatic landscape changes. These forests are also characterized by elevated proportions of rare species, which are the first to become extinct under the increasing and cumulative impacts. Given this scenario, a precise quantification of the biotic responses to environmental changes has become urgent. Moreover, we need to develop predictive approaches capable of identifying the consequences of species extinction to the structure of communities and to ecosystem functioning. Biodiversity should thus be considered in its several facets. Assessing the diversity and distribution of functional traits within species assemblages (i.e., functional structure) is a promising perspective to investigate these changes in ecosystems. In this context, the present study focused on a vulnerable and species-rich group: Amazon stream fishes. Our main objectives included: 1) determining the mechanistic pathways through which land use affects the functional structure of stream fish assemblages in the human-modified mid-eastern Amazon; and 2) investigating the possible consequences of the extinction of rare species on the functional structure of stream fish assemblages. To achieve the first goal, we sampled fish in 94 streams, and characterized stream habitat conditions and key landscape variables, including density of road crossings (i.e., riverscape fragmentation), degree of deforestation, and agricultural land use intensification. 141 species were functionally characterized using ecomorphological traits describing feeding, locomotion, and habitat preferences. We found that multiple drivers operating at different spatial scales influence stream condition and the functional structure of the fish assemblages. Riparian deforestation increased submerged vegetation, which reduced the functional evenness of assemblages (i.e., domination of a few trait combinations). Fragmentation upstream from sampling sites and deforestation altered channel morphology and stream bottom, changing the assemblage functional identity. Fragmentation downstream from sites reduced functional richness, evenness and divergence, suggesting a reduction in the range of niches filled and a functional homogenization of local assemblages. To achieve the second goal of the study, we sampled 320 streams along the main tributaries of the Amazon Basin, and functionally characterized all 395 fish species found in the samples. We then built an integrative measure of species rarity (i.e., by combining local abundance, geographic range, and habitat breadth) and assessed the contribution of rare species to complementary facets of assemblage functional structure using realistic scenarios of species loss. To enhance the generality of our findings, we applied this framework to other two sets of tropical assemblages: trees from French Guiana, and birds from the Australian Wet Tropics. We show that rare species have the most extreme and unique combinations of traits for the three taxonomic groups, and detected disproportionate impacts of rare species potential extinction on the functional structure of the assemblages. These results justify the application of the precautionary principle for tropical biodiversity conservation, despite the expected buffering effects provided by functional redundancy in such species-rich systems. Overall, we believe that this study gives important insights to improving the management and conservation of tropical biodiversity.

RESUMO

ESTRUTURA FUNCIONAL E CONSERVAÇÃO DE ASSEMBLEIAS DE PEIXES DE RIACHOS NA AMAZÔNIA BRASILEIRA

Os ecossistemas da Terra estão enfrentando níveis de perturbações antropogênicas sem precedentes. As florestas tropicais, que sustentam enorme diversidade de espécies, sofrem as mais severas alterações de paisagem na atualidade. Essas florestas abrigam uma elevada proporção de espécies raras, que tendem a ser as primeiras a se extinguir em decorrência dos impactos ambientais. Diante desse cenário, quantificações precisas das respostas bióticas frente às mudanças ambientais tornam-se urgentes. Mais do que isso, é necessário desenvolver abordagens preditivas capazes de identificar as consequências da extinção de espécies para a estrutura das assembleias e para o funcionamento dos ecossistemas. Portanto, a biodiversidade deve ser investigada em suas múltiplas facetas. A avaliação da diversidade e distribuição dos atributos funcionais das espécies nas assembleias (i.e., estrutura funcional) é uma perspectiva promissora para investigar tais mudanças nos ecossistemas. Nesse contexto, o presente estudo focou em um grupo altamente vulnerável e rico em espécies: os peixes de riachos da Amazônia. Nossos principais objetivos foram: 1) determinar os mecanismos e vias pelos quais o uso da terra afeta a estrutura funcional de assembleias de peixes de riachos em áreas antropizadas do centro-leste da Amazônia; e 2) investigar as consequências da perda potencial de espécies raras na estrutura funcional de assembleias de peixes de riachos. Para alcançar o primeiro objetivo, amostramos peixes em 94 riachos, e avaliamos características do hábitat local e variáveis-chave da paisagem, como a densidade de estradas que cruzam os riachos (i.e., fragmentação fluvial), o nível de desmatamento, e a intensificação da agricultura. 141 espécies foram caracterizadas funcionalmente a partir de atributos ecomorfológicos relacionados à alimentação, locomoção, e hábitat preferencial. Observamos que múltiplos determinantes, operando em diferentes escalas espaciais, influenciam as condições físicas dos riachos e a estrutura funcional das assembleias de peixes. A remoção da mata ripária aumentou a vegetação submersa, o que levou à redução da regularidade funcional das assembleias (i.e., dominância de algumas poucas combinações de atributos funcionais). A fragmentação a montante dos pontos amostrais e o desmatamento alteraram a morfologia do canal e a estrutura do leito dos riachos, levando a mudanças na identidade funcional das assembleias. A fragmentação a jusante dos pontos amostrais reduziu a riqueza, a regularidade e a divergência funcional, sugerindo uma redução na amplitude de nichos ocupados e uma homogeneização funcional das assembleias locais. Para alcançar o segundo objetivo deste estudo, amostramos 320 riachos ao longo dos principais tributários da Bacia Amazônica, e caracterizamos funcionalmente as 395 espécies de peixes amostradas. Criamos uma medida do grau de raridade das espécies (combinando abundância local, amplitude geográfica, e amplitude de hábitat) e avaliamos a contribuição de espécies raras para diferentes facetas da estrutura funcional das assembleias utilizando cenários realísticos de perda de espécies. Para aumentar o potencial de generalização dos nossos resultados, aplicamos esses procedimentos a duas outras comunidades tropicais: árvores da Guiana Francesa, e aves dos Trópicos Úmidos Australianos. Demonstramos para os três grupos taxonômicos que espécies raras apresentam as combinações mais extremas e únicas de atributos funcionais, e detectamos impactos desproporcionais na estrutura funcional das assembleias com a potencial extinção de espécies raras. Tais resultados justificam a aplicação do princípio da precaução na conservação da biodiversidade tropical, apesar da aparente garantia promovida pela redundância funcional esperada nesses sistemas ricos em espécies. Acreditamos que este estudo fornece importantes subsídios para a melhoria da gestão e conservação da biodiversidade tropical.

RESUMÉ

LA STRUCTURE FONCTIONNELLE ET LA CONSERVATION DES COMMUNAUTÉS DE POISSONS DES RUISSEAUX EN AMAZONIE BRÉSILIENNE

Tous les écosystèmes sur Terre sont confrontés à des niveaux de perturbations anthropiques sans précédent. Les forêts tropicales qui abritent une grande diversité d'espèces souffrent actuellement des changements de paysage les plus graves. Ces forêts sont aussi caractérisées par une forte proportion d'espèces rares, qui sont les premières à s'éteindre sous ses impacts croissants. Compte tenu de ce scénario, une quantification précise des réponses biotiques aux changements environnementaux est devenue urgente. Plus que cela, il faut développer des approches prédictives, capables d'identifier les conséquences de l'extinction des espèces sur la structure des communautés et sur le fonctionnement des écosystèmes. La biodiversité doit donc être considérée à travers ses multiples facettes. L'évaluation de la diversité et de la distribution des traits fonctionnels des espèces au sein des communautés (la structure fonctionnelle) est une perspective prometteuse pour étudier ces changements dans les écosystèmes. Dans ce contexte, cette étude porte sur un groupe vulnérable et riche en espèces: les poissons des ruisseaux Amazoniens. Nos principaux objectifs sont: 1) déterminer des voies par lesquelles les changements de paysage affectent la structure fonctionnelle des communautés de poissons des ruisseaux dans les régions perturbées du centre-est de l'Amazonie; et 2) examiner les conséquences des extinctions des espèces rares sur la structure fonctionnelle des communautés de poissons de ces ruisseaux. Pour atteindre le premier objectif, nous avons échantillonné 94 ruisseaux, et caractérisé les conditions de l'habitat et du paysage, y compris la densité des points de passage des routes (fragmentation) et les niveaux de déforestation et d'intensification agricole. 141 espèces ont été caractérisées fonctionnellement à l'aide de traits écomorphologiques décrivant l'alimentation, la locomotion et l'habitat préférentiel. Nous avons constaté que plusieurs prédicteurs à différentes échelles spatiales influencent les conditions des ruisseaux et la structure fonctionnelle des communautés. La déforestation augmente la végétation immergée, ce qui réduit la régularité fonctionnelle des communautés (domination de quelques combinaisons de traits). La fragmentation en amont de sites et la déforestation modifient la morphologie et le fond des ruisseaux, et changent l'identité fonctionnelle des communautés. La fragmentation en aval de sites réduit la richesse, la régularité et la divergence fonctionnelle, ce qui suggère une diminution de l'amplitude des niches remplies et une homogénéisation fonctionnelle des communautés. Pour atteindre le deuxième objectif de l'étude, nous avons échantillonné 320 ruisseaux le long des principaux affluents du bassin de l'Amazone, et nous avons caractérisé fonctionnellement les 395 espèces des poissons. Nous avons construit une mesure de rareté des espèces (combinant l'abondance locale, l'aire géographique, et la gamme de l'habitat) et nous avons évalué la contribution des espèces rares à différentes facettes de la structure fonctionnelle en utilisant des scénarios réalistes de perte d'espèces. Pour améliorer la généralité de nos constatations, nous avons appliqué ces procédures à deux autres communautés tropicales: des arbres de Guyane Française, et des oiseaux des Tropiques Humides Australiens. Nous avons montré pour les trois groupes taxonomiques que les espèces rares ont les combinaisons de traits les plus extrêmes et les plus uniques, et nous avons détecté des impacts disproportionnés sur la structure fonctionnelle des communautés en fonction de l'extinction simulée des espèces rares. Ces résultats justifient l'application du principe de précaution pour la conservation de la biodiversité tropicale, malgré l'assurance apparente fournie par ces systèmes riches en espèces. Nous croyons que cette étude donne des indications importantes pour améliorer la gestion et la conservation de la biodiversité tropicale.

PREFACE

This PhD thesis addresses the conservation of stream fish assemblages in the Amazon, focusing on the functional structure of the species assemblages. The study intends to give insights and guidance to the management of assemblages and ecosystems based on a functional perspective. Its main contribution relies on the fact that the functional structure of assemblages was scarcely linked with conservation issues, such as the importance of rare species and the multiple impacts of anthropogenic activities on this biodiversity facet. Filling this research gap is especially critical for tropical ecosystems, which are facing unprecedented levels of human-induced disturbances along with accelerating economic growth, and where a large number of species within assemblages are rare. The thesis is divided as follows: a general introduction, briefly focusing on key aspects that form the background of the study; two chapters already formatted to submission to specific scientific journals; and a synthesis of main outcomes of the thesis and some insights for further studies on the theme.

The first chapter aims to understand the mechanistic pathways through which land use affects the functional structure of stream fish assemblages. The study was conducted across 94 headwater streams from two regions in the mid-eastern Brazilian Amazon. The dataset comprises landscape predictors, instream habitat characterization, local fish abundances and functional trait information (related to food acquisition, locomotion, and habitat preferences) for 141 fish species.

In the second chapter, using realistic scenarios of species loss, we investigated the possible consequences of rare species extinctions on the functional structure of assemblages. We initially used a database of standardized fish surveys from 320 rainforest streams in the Brazilian Amazon, comprising habitat characterization, local abundance and functional trait information for 395 fish species. To improve the potential of generalization of the study, in a second step we invited other collaborators and included two complementary datasets: an inventory of tropical trees (262 species functionally characterized by traits describing leaf and wood characteristics) conducted in 36 standard plots across French Guiana; and an extensive sampling of birds from the Australian Wet Tropics, comprising 180 permanent transects distributed across 47 sub-regions, where 86 species were functionally characterized by traits describing key aspects of bird's life history and behaviour.

TABLE OF CONTENTS

INTRODUCTION.....	1
Landscape changes and conservation in the Amazon	1
Species rarity in the tropics	4
The Amazonian freshwaters & stream fishes	6
The functional approach of biodiversity	7
OBJECTIVES.....	10
CHAPTER 1: Disentangling the multiple effects of land use on the functional structure of fish assemblages in Amazon streams	11
Abstract.....	13
Introduction	14
Methods	16
Study area	16
Landscape assessment	17
Instream physical habitat structure	18
Fish sampling.....	18
Functional structure of fish assemblages.....	19
Data analyses	20
Results	23
Landscape and habitat characteristics.....	23
Ichthyofauna	23
Land use effects on fish functional structure.....	24
Discussion.....	32
Land use, instream habitat and the functional structure of assemblages.....	33
Loss of connectivity and the functional structure of assemblages	35
Study limitations and general recommendations	36
Conclusions	37
References	38
Supporting information.....	47
CHAPTER 2: Rare species over-contribute to the functional structure of species assemblages.....	70
Abstract.....	72
Introduction	73
Methods	74
Datasets.....	74
Rarity assessment	77
Functional structure of species assemblages	79
Scenarios of species loss.....	80
Results	81
Discussion.....	84
References	91
Supporting information.....	98
SYNTHESIS.....	121
REFERENCES	124
APPENDIX.....	146

LIST OF TABLES

CHAPTER 1

Table 1: Mean and range (minimum – maximum) of the landscape and instream physical habitat variables used in the Structural Equation Model from Santarém (n = 40) and Paragominas (n = 49) sites.....	24
Table 2: Overall model explanation (R^2 values from the Structural Equation Model) for each habitat metric and biodiversity index for Santarém (STM) and Paragominas (PGM) streams. Order from higher to lower explanation, considering mean R^2 between regions.....	25
Table 3: Total and indirect effects (mediated by instream conditions) of land use on the structure of stream fish assemblages in Santarém (n=40). S: taxonomic richness; J: taxonomic evenness; FRic: functional richness; FEve: Functional evenness; FDiv: Functional divergence; FSpe: Functional specialization; CWM1-4: Functional identity.	28
Table 4: Total and indirect effects (mediated by instream conditions) of land use on the structure of stream fish assemblages in Paragominas (n=49). S: taxonomic richness; J: taxonomic evenness; FRic: functional richness; FEve: Functional evenness; FDiv: Functional divergence; FSpe: Functional specialization; FOri: Functional originality; CWM1-4: Functional identity.....	32
Table S1: List of the 18 functional traits measured for stream fishes from the eastern Amazon.....	65

CHAPTER 2

Table A1.1: Environmental parameters measured in each of the 320 streams sampled for fishes in the Brazilian Amazon.....	98
Table A1.2: Environmental parameters measured in each of the 36 rainforest plots sampled for trees in French Guiana.	99
Table A2.1: List of the 18 functional traits measured for stream fishes from the Brazilian Amazon.....	101
Table A2.2: List of the 15 functional traits measured for rainforest trees from French Guiana.	103
Table A2.3: List of the seven functional traits (life history and behavior) assessed for birds from the Australian Wet Tropics (AWT).	104
Table S1: Friedman paired test (χ^2 ; p-value) comparing the functional structure – FS (functional richness – FRic, specialization – FSpe, and originality – FOri) of local assemblages (stream fishes from the Amazon, rainforest trees from French Guiana, and birds from Australian Wet Tropics) after species-loss simulations.....	109
Table S2: List of functions and R-packages for computations.....	110

LIST OF FIGURES

INTRODUCTION

- Figure 1:** The Amazon Forest covers a vast portion of the equatorial belt of South America, extending across nine countries. 2
- Figure 2:** Examples of important causes of human-induced landscape changes in the Amazon. 3
- Figure 3:** Scheme representing the different forms of rarity. 4
- Figure 4:** Headwater streams in the Amazon. 7
- Figure 5:** Diversity of species and functional traits of stream fishes in the Amazon. 8

CHAPTER 1

- Figure 1:** Sampling sites distributed across gradients of land use in Santarém and Paragominas, mid-eastern Brazilian Amazon. 17
- Figure 2:** Hypothesized model tested using Structural Equation Modeling, indicating the expected pathways for the effects of land cover and riverscape fragmentation on the structure of Amazon stream fish assemblages. 22
- Figure 3:** Structural Equation Model diagram showing the effects of land cover, riverscape fragmentation, instream habitat characteristics and natural landscape factors on the structure of stream fish assemblages in Santarém region. 27
- Figure 4:** Position of the predominant state of each ecomorphological trait along each Principal Coordinate (PCoA) axis that composes the multidimensional functional spaces for fish species pools in Santarém and Paragominas sites. 29
- Figure 5:** Structural Equation Model diagram showing the effects of land cover, riverscape fragmentation, instream habitat characteristics and natural landscape factors on the structure of stream fish assemblages in Paragominas region. 31
- Figure S1:** Representation of the three different spatial scales assessed for landscape analyses: the whole catchment upstream from sample site (“catchment”); 100-m wide buffer along the entire drainage network upstream from sample site (“network riparian”), and 100-m wide buffer around the sampled site (“local riparian”). 47
- Figure S2:** Schematic representation of the sampled stream stretch. A total of 11 transects and 10 longitudinal sections of 15m were established. 47
- Figure S3:** Non-metric Multidimensional Scaling (NMDS) ordination of sites from Santarém (n = 40; green dots) and from Paragominas (n = 49; dark gray dots) based on fish species abundance (A) and presence/absence within streams (B). 48

Figure S4: Four-dimensional representation of the functional space of the global pool (141 species) of stream fishes from Santarém and Paragominas, mid-eastern Amazon basin.	48
Figure S5: Correlation between R^2 values from Santarém (STM) and Paragominas (PGM) structural equation models.	49
Figure S6: Four-dimensional representation of the functional space of the regional pool of stream fishes from Santarém (67 species).	50
Figure S7: Four-dimensional representation of the functional space of the regional pool of stream fishes from Paragominas (112 species).	57
Figure S8: Morphological traits measured for fish from digital pictures and with digital caliper.	65

CHAPTER 2

Figure 1: Hypothetical scenarios for the contribution of rare species to the functional structure of species assemblages.	75
Figure 2: Functional structure (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) supported by rare and common species of three tropical species assemblages: stream fishes from the Brazilian Amazon, rainforest trees from French Guiana, and birds from the Australian Wet Tropics.	82
Figure 3: Impact of regional species extinction of the rarest species on the functional structure (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) of three tropical assemblages: stream fishes from the Brazilian Amazon, rainforest trees from French Guiana, and birds from the Australian Wet Tropics.	83
Figure 4: Impact of local species extinction on the functional structure – FS (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) of local assemblages of stream fishes from the Brazilian Amazon, rainforest trees from French Guiana, and birds from the Australian Wet Tropics.	84
Figure 5: Multidimensional functional spaces built with the species pool of three tropical assemblages: stream fishes from the Brazilian Amazon (395 species), rainforest trees from French Guiana (262), and birds from the Australian Wet Tropics (86).	87
Figure A1.1: Schema of local habitat assessment for Amazonian fishes showing where each environmental parameter was measured at the streams.	99
Figure A2.1: Morphological traits measured for fish from digital pictures and with digital caliper.	101
Figure A3.1: Correlation between functional indices (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) supported by each commonness class when the fish functional space was built with four (abscissas), three (ordinates in left figures), and five (ordinates in right figures) dimensions. Commonness classes contain 10% of the	

global pool of species (395 stream fishes from the Brazilian Amazon) and are ordered from the rarest to the commonest species. 106

Figure A3.2: Correlation between functional indices (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) supported by each commonness class when the tree functional space was built with nine (abscissas), eight (ordinates in left figures), and ten (ordinates in right figures) dimensions. Commonness classes contain 10% of the global pool of species (262 rainforest trees from French Guiana) and are ordered from the rarest to the commonest species. 107

Figure A3.3: Correlation between functional indices (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) supported by each commonness class when the bird functional space was built with five (abscissas), four (ordinates in left figures), and six (ordinates in right figures) dimensions. Commonness classes contain 10% of the global pool of species (86 birds from the Australian Wet Tropics) and are ordered from the rarest to the commonest species. 108

Figure S1: Geographic locations sampled for rainforest trees from French Guiana (36 plots represented by black cross), stream fishes from the Brazilian Amazon (320 sites represented by black dots), and birds from the Australian Wet Tropics (47 subregions)..... 111

Figure S2: Four-dimensional functional space of the regional pool of stream fishes from the Amazon (395 species). 112

Figure S3: Nine-dimensional functional space of the regional pool of rainforest trees from French Guiana (262 species). 113

Figure S4: Five-dimensional functional space of the regional pool of birds from the Australian Wet Tropics (86 species). 116

INTRODUCTION

Landscape changes and conservation in the Amazon

All ecosystems on Earth are facing unprecedented levels of disturbance (Vitousek *et al.* 1997), and studies suggest that the current huge rates of species loss are inducing a sixth extinction crisis (Barnosky *et al.* 2011). At the forefront of this environmental crisis are the tropical biomes, which typically support the species-richest biotas but, at the same time, currently suffer the most acute landscape changes (Nepstad *et al.* 1999; Laurance & Peres 2006; FAO 2011). Most of tropical forests are distributed in developing countries, where the balance between economic growth and biodiversity conservation is conflicting (Soares-Filho *et al.* 2014), with the former often favored over the latter. Aligned with the economic growth are the land scarcity and the increasing resource demands from a larger human population (Lambim & Meyfroidt 2011).

Agro-industrial activities remove hundreds of thousands of hectares of tropical forest yearly (*c.* 50,000 km² according to Hansen *et al.* 2010), and even relatively well-preserved biomes such as the Amazon are severely threatened. The Amazon is home to more than 30 million people and provides locally, regionally and globally significant human-welfare benefits, including economic goods (e.g., timber and agricultural products) and non-market ecosystem services, such as climatic regulation and biodiversity conservation (Malhi *et al.* 2007; Peres *et al.* 2010; FAO 2011). Dealing with this complex social-ecological balance is currently a major sustainability challenge in the region (Gardner *et al.* 2013; see Appendix).

Although still comprising the most extensive undisturbed tropical forest on Earth, the Amazon exhibits the highest absolute rates of deforestation (Hansen *et al.* 2008). Particularly at the Brazilian Legal Amazon, about 20% (*c.* 750,000 km²) of the original forest cover had been cleared by 2012 (INPE 2013). This degradation process has initially accelerated with road-building and frontier-colonization projects in the 1970s (Peres *et al.* 2010). These projects, summed to the more recent massive agricultural expansion and intensification, resulted in the so-called “arc of deforestation”, a conspicuous and broad degraded area extending from the southern to the northeastern portion of the Amazon (Fig. 1). Beyond land use changes directly associated to agriculture/livestock activities and fragmentation by road construction, there are several other widespread important forms of landscape alteration in the

Amazon, such as logging, mining, hydroelectric dams and urbanization (Gascon *et al.* 2001; Fearnside 2006; Fig. 2).

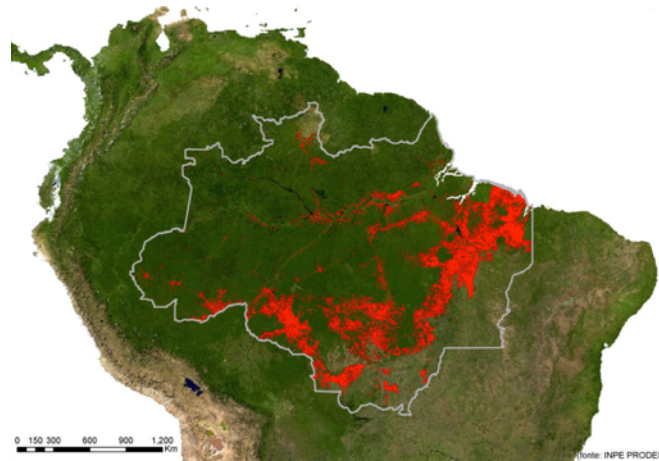


Figure 1: The Amazon Forest covers a vast portion of the equatorial belt of South America, extending across nine countries (*c.* 7.6 million km²). Although comprising the species-richest and most extensive undisturbed tropical forest on Earth, it exhibits the highest absolute rates of deforestation, as illustrated by the “arc of deforestation” (in red), a broad degraded area extending from the southern to the northeastern portion of the Brazilian Amazon (delimited by the gray polygon). Image source: INPE PRODES.

Some particularities of the geography, paleoecology and human-settlement history in the Amazon forest are evoked to explain its enormous species richness and low extinction rates throughout geological and ecological time. At the same time, these characteristics suggest that Amazonian biodiversity should be highly sensitive to contemporary landscape changes (Peres *et al.* 2010). Firstly, given its geographic position (*i.e.*, in the middle of a wide continent, close the sea level, near Equator, and “blocked” by the Andean rain-shadow which ensured a continuous precipitation recycling) the region has been historically submitted to a high climatic stability (Bush 1994; Morley 2000; Stropp *et al.* 2009). Secondly, geological and paleobotanical evidence has shown that most of the Amazon lowlands remained under a dense forest cover throughout at least the last two glacial and interglacial cycles (Colinvaux *et al.* 2000). Finally, apart from areas near the main rivers, there is no evidence of large landscape changes promoted by Pre-Columbian human populations (Bush & Silman 2007). Therefore, the evolutionary history of most Amazonian species has been predominately shaped in a relatively stable environment, with almost no anthropogenic pressures, and across extensive closed-canopy humid forests (Peres *et al.* 2010). These combined characteristics may explain the elevated proportion of true forest specialist groups, and the potential high vulnerability (*e.g.*, low resistance and resilience) of the biological assemblages facing the

current landscape changes in the region (Peres *et al.* 2010). This somewhat worrying scenario calls for the urgent need to improve our ability to understand how Amazonian biodiversity responds to the increasing human-induced environmental impacts.

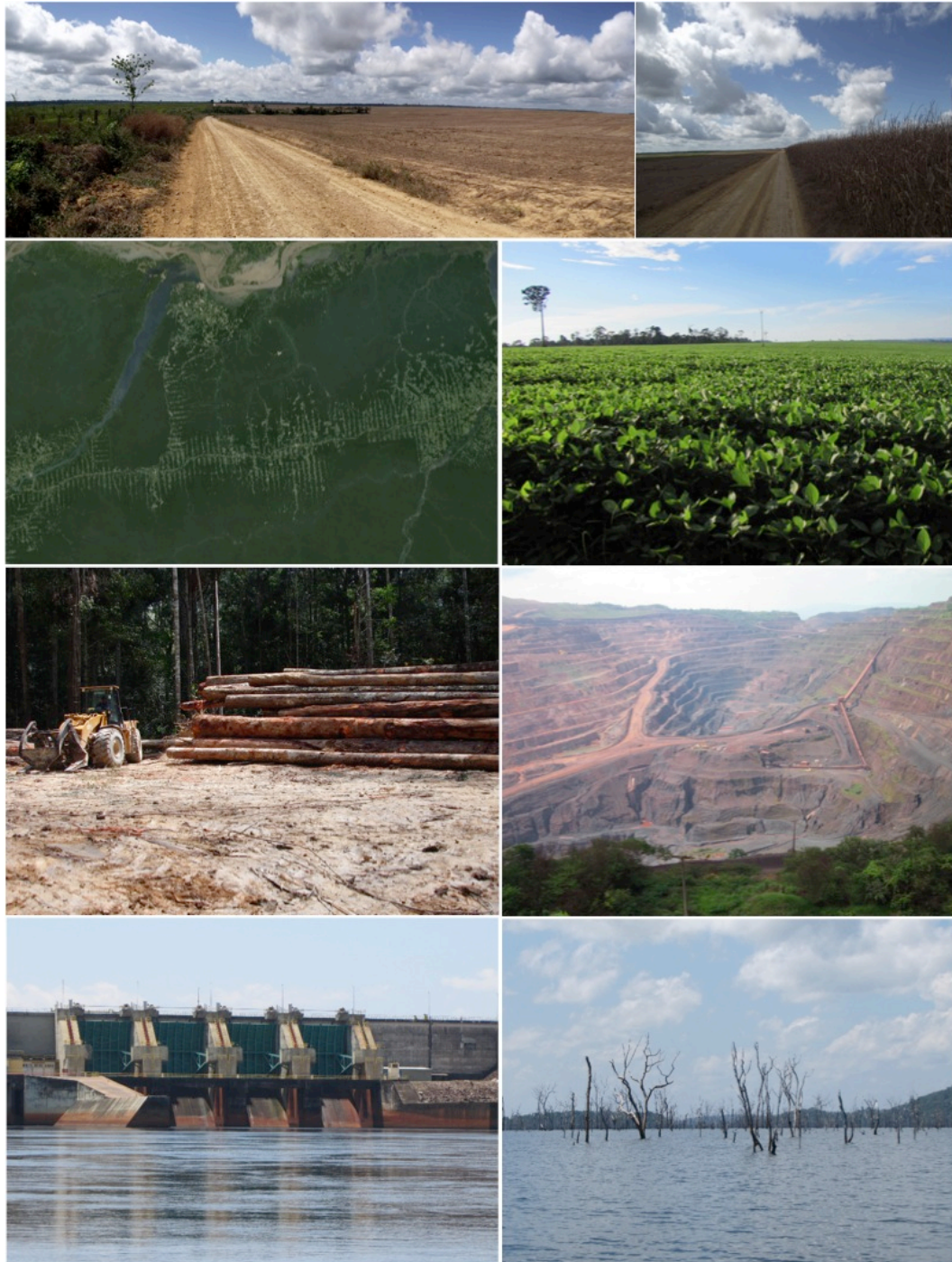


Figure 2: Examples of important causes of human-induced landscape changes in the Amazon: fragmentation by roads, forming the typically “fish-bone” pattern of occupation in the region; soya bean croplands, leading to extensive deforested areas mainly across the “arc of deforestation”; logging, acting in several areas, even in the central or western Amazonia; mining of iron and bauxite; several hydroelectric dams under construction, drastically modifying the aquatic systems of the Amazon. Image source: M. Silva, R. Leitão, D. Kasper, GoogleEarth (Landsat).

Species rarity in the tropics

A widely recognized pattern in tropical ecosystems is the significant proportion of rare species within assemblages (with qualitative indications dating back to Bates, Darwin, and Wallace in the second half of the 1800s). Species can be considered rare when they have small population sizes, restricted geographic ranges, or narrow habitat tolerances. These combined characteristics define several forms of rarity (Rabinowitz 1981; Fig. 3), with the most extreme case being represented by species known for only one individual (i.e. singletons). Despite the possible undersampling bias, singletons are frequently found in the tropics (e.g., *c.* 30% of arthropod were singletons in moist forest surveys in Guiana; Coddington *et al.* 2009).

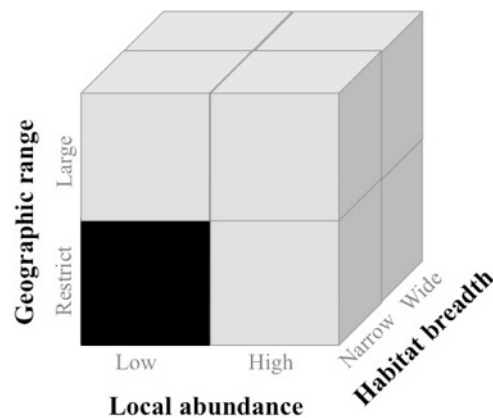


Figure 3: Scheme representing the different forms of rarity (adapted from Rabinowitz 1981). Species at the lower front left (black square) combine all three components of rarity (low local abundance, restrict geographic range and narrow habitat). These species are likely more vulnerable to a variety of disturbances and, consequently, more prone to extinction.

Particularly for the Amazon forest, increasing evidences suggest that a high portion of the species is locally and globally rare (Hubbell 2013; but see Pitman *et al.* 1999). For instance, an extensive assessment across the entire Amazon Basin and Guiana Shield showed that only 227 (1.4%, the so-called hyper-dominant) of the estimated 16,000 tree species accounts for half of all individuals (ter Steege *et al.* 2013). Within the same dataset, a great proportion (*c.* 37.5%) of the species could be classified as hyper-rare (i.e., those with fewer than 1000 individuals in total, according to Hubbell 2013 and ter Steege *et al.* 2013). Through a long-time monthly sampling of fish assemblages in floodplain lakes from the mid-western Amazon Basin, Hercos *et al.* (2012) classified 88% of the species as rare (i.e., the authors considered as rare if the species had less than 1% of the total number of individuals); of these, 26% are represented only as singletons.

The causes of rarity are still poorly understood and are an important subject in evolution and ecology debates (Ricklefs 2000). However, there is a global consensus that rarity is a primary component of extinction process (Olden *et al.* 2008), and the different combinations of rarity forms define different levels of extinction risk (Harnik *et al.* 2012). Compared to abundant and widespread species, rare species have greater susceptibility to both natural (e.g. environmental stochasticity) and human-induced disturbances such as overexploitation, habitat loss, or global environmental changes (Purvis *et al.* 2000; Davies *et al.* 2004; Lavergne *et al.* 2005; Sekercioglu *et al.* 2008). For instance, when confronting the distribution of rare tree species with projections of landscape changes in the Brazilian Amazon, Hubbell (2013) revealed a dramatic scenario: about half of the species with populations below a total abundance of 10^4 individuals could be at high extinction risk by midcentury, or have actually already gone extinct from habitat loss. Rare species have thus received significant attention from conservation biologists, being considered an important criterion to take into account in defining the conservation status of the species or in developing management plans (Mace *et al.* 2008; Hercos *et al.* 2012). Contrasting with this important conservation aspect, there is a substantial lack of precise distributional/biogeographic data in tropical regions (Ricklefs 2000). Importantly, a primary cause of this gap is the deficiency of basic alpha-taxonomy for several tropical groups; thus, a significant amount of rare species may be going extinct even before they can be found and scientifically described.

This scenario would deserve even further concern if rare species have critical or irreplaceable roles within communities and ecosystems. A recent study showed that in three regional species pools (coral reef fishes, tropical trees, and alpine plants) the most distinct combinations of traits (related to life history, use of resources, and leaf and wood economics) are predominately supported by rare species (Mouillot *et al.* 2013a), which may suggest that they are functionally irreplaceable. Moreover, the authors revealed that species that have low functional redundancy and are likely to support the most vulnerable functions, with no other species carrying similar combinations of traits, are rarer than expected by chance. These results reinforce the importance of intensifying studies on rare species, and open critical questions about the consequences of rare species extirpations on the structure of communities and on the functioning of ecosystems.

The Amazonian freshwaters & stream fishes

Despite significant advances in the understanding of anthropogenic effects on terrestrial ecosystems (Gardner *et al.* 2007), tropical freshwaters have comparatively received less attention (Chapman and Chapman 2002). Particularly for Amazon freshwaters, the scarcity of such studies is noteworthy when considering the accelerated landscape changes and the huge biological diversity they support. Besides being the largest river system (*c.* 6.8 million km²; Goulding *et al.* 2003), the Amazon Basin contains the richest freshwater ichthyofauna in the world, estimated at *c.* 2400 species only at its Brazilian portion (J. Zuanon, pers. comm.).

In Brazil, approximately 80% of the energy used come from hydroelectric power (Internationalrivers 2010), with the Amazon comprising the greater hydropower potential (*c.* 2/3 of the total potential for the country; Bermann 2002). Hence, several colossal reservoirs were recently built, are under construction or are planned to the region (e.g., Jirau and Santo Antônio reservoirs on the Madeira River, and Belo Monte Reservoir on the Xingu River). Due to the need to comply with environmental legislation, the consequences of these impoundments to commercial fishes are becoming more evident (Torrente-Vilara *et al.* 2011; Queiroz *et al.* 2013; Kasper *et al.* 2014). However, small Amazon streams are still highly overlooked in terms of the effects of landscape alterations on fish assemblages.

Headwater streams in the Amazon (regionally known as *igarapés*) form a complex hydrological network (Junk 1983), with their vast majority running under dense forest canopies. They typically have oligotrophic and acidic waters (due to the presence of humic and fulvic acids), with the bottoms mainly composed of sand and coarse litter (Mendonça *et al.* 2005), and channel morphology often shaped by large wood debris and roots from the adjacent forest (Fig. 4). Differently from the seasonal lateral expansion-contraction of the mainstream channel typically found in the large floodplain rivers of the Amazon (i.e., flood-pulse; Junk *et al.* 1989), hydrological fluctuations in *terra firme* streams are controlled by local rainfall; stream discharge increases rapidly in response to local rainstorms and then recedes to pre-disturbance levels within a few hours (Espírito-Santo *et al.*, 2009, 2013).



Figure 4: Headwater streams in the Amazon typically run under dense forest canopy and have bottoms mainly composed of sand, coarse litter, tree roots and wood debris. Image source: R. Leitão, C. Leal.

Although small in physical dimensions, these streams account for a significant portion of freshwater ecosystems in the Amazon, and are important contributors to the regional biodiversity (e.g., during the present study, we reported several cases of >40 fish species within a single 50-m stream segment). It has been estimated that about 2,000 species of freshwater fish have yet to be described in South America, the great majority occurring in areas away from the large rivers (Castro, 1999). In fact, the intensification of ichthyofauna surveys in *terra firme* streams has been leading to taxonomic description of dozens of new species in the last decade. This huge species richness is directly accompanied by a remarkable variety of fine-tuned ecological adaptations (Fig. 5) that provide differential capabilities to explore the stream resources and to interact with other species and with the surrounding environment (Zuanon & Sazima 2004; Zuanon & Sazima 2005; Carvalho *et al.* 2006; Sazima *et al.* 2006; Zuanon *et al.* 2006a, 2006b; Carvalho *et al.* 2014). Identifying the consequences of anthropogenic impacts in such diversity of ecological functions performed by the species is a challenging but promising perspective to develop more effective conservation strategies to Amazonian stream fishes.

The functional approach of biodiversity

Given the magnitude of human-induced disturbances across ecosystems, precisely quantifying biodiversity responses to these impacts has become urgent. More than this, it is necessary to develop predictive approaches capable to identify the consequences of species extinction to the structure of communities and to ecosystem functioning and services (Mouillot *et al.* 2013b).

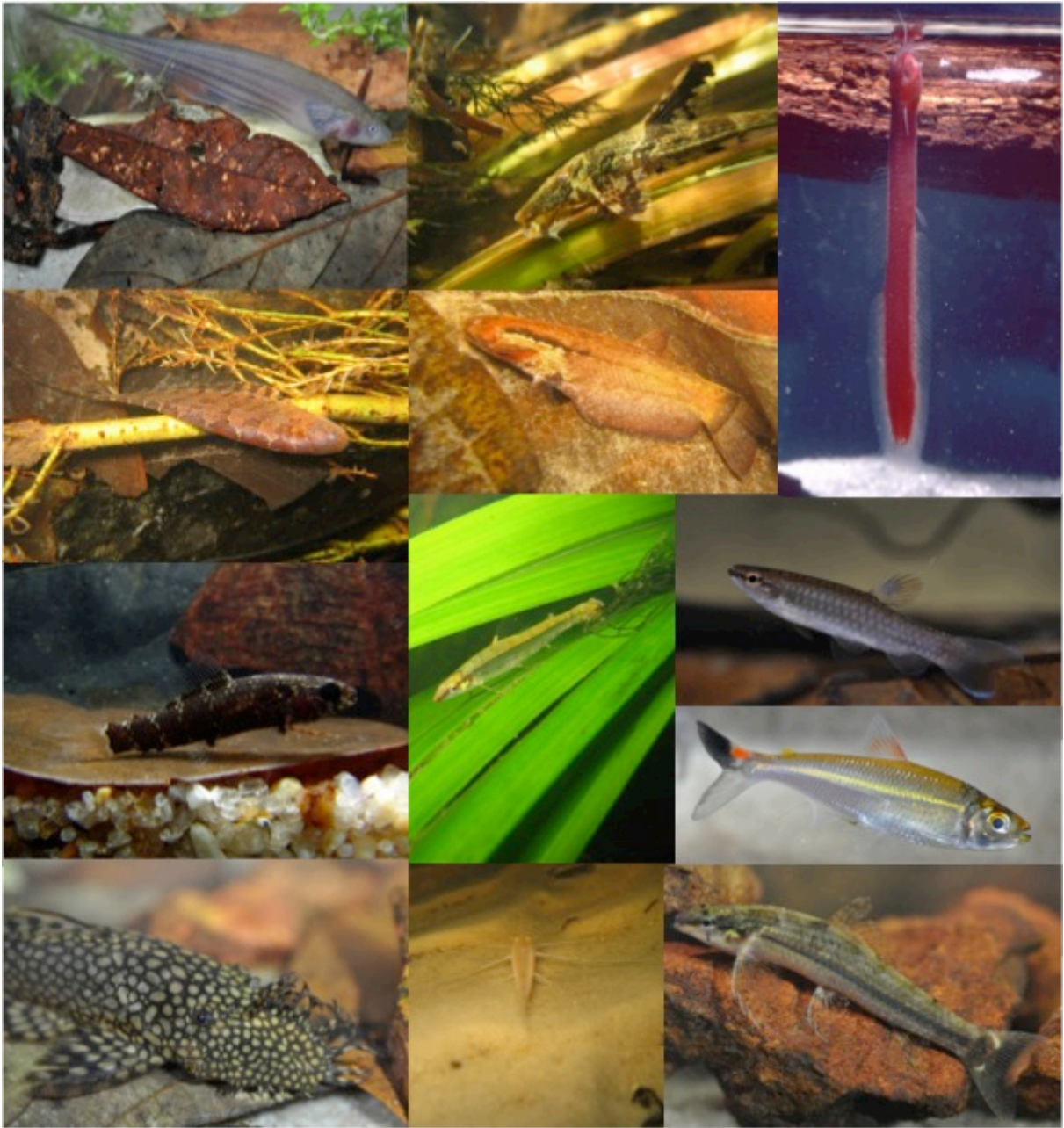


Figure 5: Diversity of species and functional traits of stream fishes in the Amazon. Image source: R. Leitão, J. Zuanon, I. Sazima, L. Carvalho.

Changes in biotic communities facing environmental disturbances were traditionally quantified using taxonomic indicators, such as species richness, relative abundances and, in a step further, species composition. However, the simple assessment of these metrics gives an incomplete view of biodiversity, because they do not take into account the evolutionary or biological/ecological differences between species (Petchey & Gaston 2002; McGill *et al.* 2006; Villéger *et al.* 2008; Cadotte & Davies 2010). Moreover, these purely taxonomic indicators were frequently unable to detect consistent responses to human-induced impacts

(Ernst *et al.* 2006). Therefore, there is an increasing awareness that biodiversity should be assessed in its multiple facets (e.g., genetic, phylogenetic, functional; Villéger *et al.* 2008; Cadotte *et al.* 2010).

In the last decade, a remarkable amount of studies have incorporated the differences between species drawing upon their functional traits (e.g., morphological, behavioral, physiological). Furthermore, better analytical tools have been developed to quantify the diversity and distribution of these traits within the species assemblages (i.e., functional diversity/structure of the assemblage; Petchey & Gaston, 2002; Mason *et al.*, 2003, 2005; Mouillot *et al.*, 2005; Cornwell *et al.*, 2006; Villéger *et al.*, 2008; Laliberté & Legendre, 2010). Currently, the functional structure of a species assemblage is seen as a multidimensional framework in which species traits and abundances can be directly considered (Villéger *et al.* 2008). Using continuous metrics not necessarily dependent of species richness, a wide range of information can be assessed, such as the extent of niche occupation and the regularity of species traits within the assemblage, the level of functional specialization and redundancy, and the individual trait contribution to the assemblage structure (Villéger *et al.* 2008; Mouillot *et al.* 2013b). Among the main advantages of the multidimensional framework, ecologists highlighted the potential: 1) to produce more generalized models, because biogeographical constraints are lessened and more direct links between organism and habitat are likely (Hoeinghaus *et al.* 2007); 2) to provide advanced warning to changes in disturbed ecosystems (i.e., not needing species loss to be reactive; Mouillot *et al.* 2013b); 3) to make more direct relationship between community structure and ecosystem functioning, because the diversity of ecological processes is more closely related to the diversity of functional traits than to the diversity of taxa itself (Petchey *et al.* 2004; Hooper *et al.* 2005; Mouillot *et al.* 2011).

Therefore, the functional approach opens countless possibilities to raise both theoretical and applied questions in ecology. Despite the promising perspectives, it was scarcely linked with conservation issues, such as the impacts of anthropogenic activities (e.g., Ernst *et al.* 2006; Flynn *et al.* 2009; Villéger *et al.* 2010; Teresa & Casatti 2012) and the consequences of rare species extinction (e.g., Jain *et al.* 2014) on the functional structure of species assemblages.

OBJECTIVES

The general objective of this study is to investigate the effects of environmental changes on the functional structure of stream fish assemblages in the Brazilian Amazon. More specifically, I intend to:

- Determine the mechanistic pathways through which land use (e.g., deforestation and riverscape fragmentation) affects the functional structure of stream fish assemblages in the mid-eastern Brazilian Amazon Basin;
- Investigate the consequences of the possible extinctions of rare species on the functional structure of stream fish assemblages in the Brazilian Amazon Basin;
- Evaluate the generality of the consequences of rare species loss among different biological assemblages (fish, plants, birds).

CHAPTER 1

Leitão, R.P.; Zuanon, J.; Leal, C.G.; Pompeu, P.S.; Gardner, T.A.; Barlow, J.; Hughes, R.M.; Kaufmann, P.R.; Kasper, D.; Ferreira, J.; Rossetti, F.; Ferraz, S., Villéger, S. & Mouillot, D. Disentangling the multiple effects of land use on the functional structure of fish assemblages in Amazon streams. Manuscript under preparation to *Ecological Applications*.

Disentangling the multiple effects of land use on the functional structure of fish assemblages in Amazon streams

Rafael P. Leitão ^{1,2}, Jansen Zuanon ³, Cecília G. Leal ^{4,6}, Paulo S. Pompeu ⁴, Toby A. Gardner ⁵, Jos Barlow ^{6,7}, Robert M. Hughes ⁸, Philip R. Kaufmann ⁹, Daniele Kasper ³, Joice Ferreira ¹⁰, Felipe Rossetti ¹¹, Silvio Ferraz ¹¹, Sébastien Villéger ² and David Mouillot ^{2,12}

Affiliations:

¹ Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, 69060–001 Manaus, Brazil.

² Laboratoire Biodiversité Marine et ses usages, UMR 9190 MARBEC CNRS–UM-IRD–IFREMER, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier, France.

³ Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, 69060–001 Manaus, Brazil.

⁴ Departamento de Biologia, Universidade Federal de Lavras, CP 3037, Lavras, Brazil.

⁵ Stockholm Environment Institute, 104 51 Stockholm, Sweden.

⁶ Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

⁷ MCTI/Museu Paraense Emílio Goeldi, CP 399, CEP 66040–170r, Belém, PA, Brazil.

⁸ Amnis Opes Institute and Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA.

⁹ Office of Research and Development, U.S. Environmental Protection Agency, 200 SW 35th St., Corvallis, Oregon, USA.

¹⁰ Embrapa Amazônia Oriental, Travessa Dr. Enéas Pinheiro, CP 48, 66095-100 Belém, Brazil.

¹¹ Escola Superior de Agricultura “Luiz Queiroz”, Universidade de São Paulo, Av. Pádua Dias, 11, Piracicaba, Brazil.

¹² Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811 Australia.

Running title: Land use effects on fish functional structure

Key-works: functional diversity; deforestation; landscape fragmentation; freshwater; tropics; Amazon Basin.

ABSTRACT

Agricultural land use is a primary source of impact to small streams. However, the causal processes involved in this relationship are complex, operating through multiple pathways and spatial scales; and the taxonomic structure of stream assemblages often shows contrasting responses to land use changes. This complexity hinders effective management of these ecosystems, and illustrates the need to examine complementary facets of biodiversity under mechanistic causal pathway perspectives. Here we present results of a multi-scale assessment of the biological condition of headwater streams in the human-modified mid-eastern Amazon, examining functional responses of fish assemblages to both landscape changes and alterations in physical instream habitat. We sampled fish in 94 stream sites in two large regions, and characterized stream habitat conditions by several physical attributes (e.g., substrate, channel morphology, bed complexity and stability) and key landscape-change variables, including density of road crossings (i.e., riverscape fragmentation), deforestation, and agricultural intensification. All 141 species were characterized in terms of their function using ecomorphological traits describing feeding, locomotion, and habitat preferences. Complementary indices were then computed to quantitatively describe the functional structure of the assemblages. Overall, we found that multiple drivers operating at different spatial scales influence stream condition and the functional structure of the fish assemblages. For instance, local riparian deforestation increased macrophyte+grass cover with subsequent reductions of the functional evenness of assemblages (i.e., increased the dominance of few trait combinations). Riverscape fragmentation upstream from sample sites and deforestation at catchment and riparian scales altered the channel morphology and the stream bottom structure, changing the functional identity of assemblages (e.g., species that use the benthic compartment were negatively affected). Fragmentation downstream from the sites reduced functional richness (i.e., losing regional connectivity potentially reduces the range of niche occupation by assemblages), and functional evenness and divergence, suggesting a trend of functional homogenization of local assemblages. These results underscore the often-unrecognised importance of some land use changes that can have marked effects on stream biodiversity. We draw on the relationships observed in our data to suggest priorities for the improved management of stream systems in the multiple-use landscapes that characterise so much of the human-modified tropics.

INTRODUCTION

Tropical ecosystems are facing high levels of human-induced disturbances, with land use being the primary cause of habitat loss driven by population and economic growth (Limburg et al. 2011). Agribusiness, mainly through pasture and cropland expansion, removes hundreds of thousands of hectares of tropical forest yearly (Hansen et al. 2010), and more than 20% of the original forest cover in the Brazilian Amazon has already been cleared (INPE 2013). Despite advances to slow this process in the last decade (e.g., creation of mega-reserves and greater incentives for farmers to meet environmental compliance), the effectiveness of further protection policies for the Amazon is being challenged (Ferreira et al. 2014, Godar et al. 2014). Riverine ecosystems are of special concern as studies have demonstrated widespread failures to comply with environmental legislation to protect riparian zones (Nunes et al. 2014), and recent modifications of the Brazilian Forest Code relaxed restoration requirements for these areas (Soares-Filho et al. 2014). Additionally, most of the national reserves target terrestrial organisms and ecosystems (Brooks et al. 2006, Frederico 2014), however, the dendritic and longitudinal structure of river networks and their linkages with multiple landscape scales demand different management strategies to succeed (Fausch et al. 2002).

Changes in land use across catchment and riparian zones are critical elements to consider for protecting habitat and conserving biodiversity, particularly for headwater streams (Allan 2004). For instance, deforestation may lead to increases in water temperature, alterations in channel structure, homogenization of streambeds by sedimentation, reduced inputs of woody debris, and shifts from heterotrophic to autotrophic energy sources (Roth et al. 1996, Allan et al. 1997, Bojsen and Barriga 2002, Sutherland et al. 2002). Besides forest clearing, stream fragmentation (e.g., by road crossings and dams) adversely affects stream ecosystems, acting either on the habitat conditions (e.g., by sediment and nutrient runoff) or directly on the organisms' dispersal (Perkin and Gido 2012, Johnson et al. 2013).

Landscape fragmentation and deforestation are known to result in significant alterations of stream communities. However, compared to the relatively well-studied temperate landscapes, the effects of land use on tropical freshwaters have received little attention (Chapman and Chapman 2002) and, particularly for stream fish assemblages in the Amazon, this represents a critical research gap (but see Bojsen and Barriga 2002). Small Amazonian streams can support enormous biodiversity (e.g., we reported several cases of >40 fish species within a

single 50-m stream segment), and are highly vulnerable to disturbance (Castello et al. 2013). Given that they naturally run under dense canopies and have oligotrophic and acidic waters, their food chains should depend strongly on allochthonous sources (Mendonça et al. 2005). Moreover, a particularity of these systems that potentially increases the impacts land use change on their fish assemblages is the relatively high stability of environmental conditions (Espírito-Santo et al. 2009). It is thus expected that they have lower levels of tolerance and resilience to disturbances compared to temperate stream ichthyofaunas, which have evolved in highly unstable and harsher environmental conditions (Walser and Bart 1999).

The consequences of land use on the structure of stream fish assemblages were initially investigated using a taxonomic perspective. However, contrasting results among studies mean that it has been extremely difficult to reach general conclusions. For instance, species richness or relative abundance were reported to increase (Lorion and Kennedy 2009), decrease (Lyons et al. 1995), or be unaffected by deforestation (Bojsen and Barriga 2002). In part, these mixed results illustrate the limitations of a purely taxonomic approach to interpret changes in the community structure caused by human activities; and there is growing awareness of the need to incorporate complementary facets of biodiversity to achieve this goal, such as the functional structure of the community (Ernst et al. 2006, Flynn et al. 2009, Villéger et al. 2010, Marzin et al. 2012, Mouillot et al. 2013, Terra et al. *in press*).

Currently, the functional structure of a community is described using complementary indices computed in a multidimensional framework accounting for species traits and abundances (Villéger et al. 2008). This framework is a powerful tool to reveal the complex nature of change in disturbed ecosystems, because it may provide advanced warning (i.e., not needing species loss to be reactive; Mouillot et al. 2013) and considers traits of both common and rare species (which often account for high proportions of assemblage richness, but are often overlooked in taxonomic assessments). Finally, the diversity of ecological processes is more closely related to the diversity of functional traits within communities than to the diversity of taxa *per se* (Hooper et al. 2005). Therefore, changing the functional structure of communities may directly reflect changes in ecosystem functioning (Petchey et al. 2004, Mouillot et al. 2011). Despite these promising perspectives, assessments of land use effects on the multidimensional functional structure of stream fish assemblages are still highly overlooked (e.g., Casatti et al. 2012, Teresa and Casatti 2012), especially in tropical species-rich areas.

Here we investigate how riverscape fragmentation and deforestation, mediated by alterations in instream habitat, affect the different facets of the functional structure of fish assemblages in Amazon streams. The multifaceted nature of these relationships is an unavoidable challenge in our investigation. Both environmental and biological responses vary as a function of the spatial scale at which they are assessed (Allan et al. 1997, Mantyka-Pringle et al. 2014), and changes expected to be associated with land use may also be attributed to covarying natural gradients (Allan 2004, Whittier et al. 2006). To deal with these complexities we adopted structural equation modeling procedures, which enable joint consideration of predictors at different scales (e.g., catchment, riparian, instream habitat) to identify mechanistic causal pathways of land use on assemblage structure (e.g., Riseng et al. 2011). Therefore, we believe that our study is an important step forward in managing and conserving Amazonian stream fishes.

METHODS

Study area

This study is part of the Sustainable Amazon Network (*Rede Amazônia Sustentável*), a multidisciplinary research initiative focussed on assessing both the social and ecological dimensions of land-use sustainability in the mid-eastern Brazilian Amazon (see Gardner et al. 2013). We sampled 94 headwater stream sites (150 m long) from two regions: Santarém-Belterra (STM), located near the confluence of Amazonas and Tapajós rivers; and Paragominas (PGM), in the lower Amazon Basin. The sampling design encompassed 45 sites in STM, draining to the Curuá-Una, Tapajós, or straight to the Amazonas Rivers; and 49 sites in PGM, in the Gurupi and Capim River Basins. We sampled during the Amazonian dry season in STM (July-August 2010) and PGM (June-August 2011). Samples were distributed along a gradient of previously known anthropogenic impacts based primarily on the amount of remnant forest cover in the contributing drainage area of each site (Gardner et al. 2013; Fig. 1). The two regions have differing histories of human land use and occupation, with STM occupied by non-indigenous settlers for centuries (since 1661), and PGM only recently colonized (since 1959). The landscapes are characterized as mosaics of well-established mechanized agriculture, local and regional centres for cattle markets, silviculture, small landowner colonies, as well as regenerating secondary forests, and disturbed and undisturbed primary forests, the latter mostly found in officially protected areas (e.g., Tapajós National Forest).

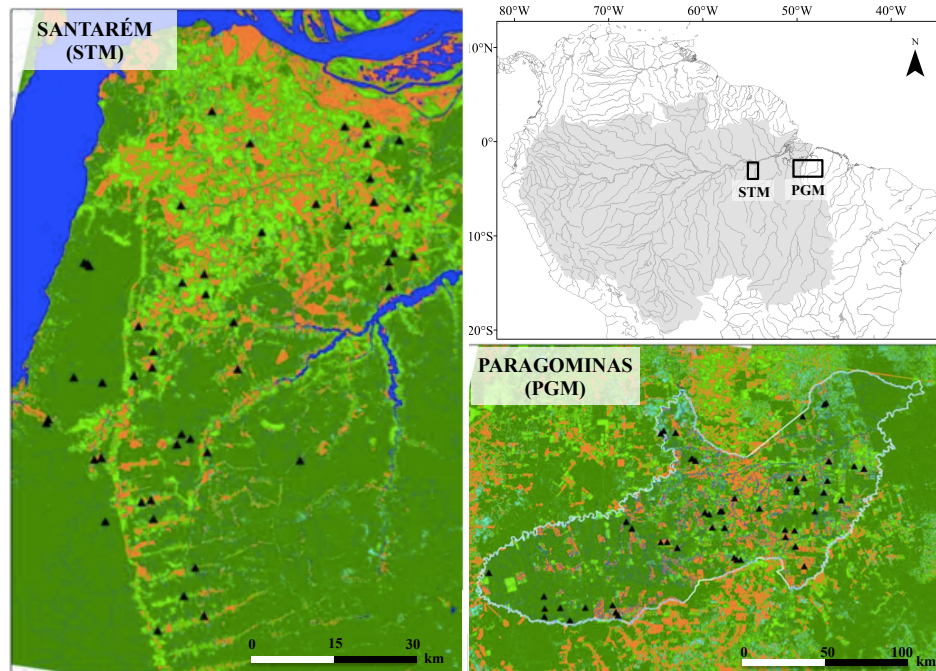


FIG. 1. Sampling sites (black triangles) distributed across gradients of land use in Santarém (*c.* 1 million ha) and Paragominas (*c.* 1.9 million ha), mid-eastern Brazilian Amazon. Land use classification derived from Landsat 2010 image, showing primary forest (dark green), secondary forest (light green), and deforested areas (orange). Gray polygon in the top right map indicates the Amazon Basin.

Landscape assessment

We analysed landscape features at three different spatial scales (Appendix A): the whole catchment upstream from the site (herein after “catchment”); a 100-m wide buffer along the entire drainage network upstream from the site (“network riparian”); and a 100-m wide buffer around the sampled site (“local riparian”). Catchment boundaries and area (ha) were obtained using digital elevation models for STM (Shuttle Radar Topography Mission images with 90 m resolution; NASA) and for PGM (TopoData with 30 m resolution; Instituto Nacional de Pesquisas Espaciais, Brazil). The drainage network was extracted using the hydrological model ArcSWAT (Soil and Water Assessment Tool extension for ArcGis). The percentage of deforestation at each of the three spatial scales was obtained using a land use map (Landsat TM and ETM+ images, 30 m resolution, year 2010). We defined deforestation as the sum of cleared areas in 2010, deforested primary forest areas in the past, old-regeneration-deforestation (deforestation of secondary forest areas in baseline year – 1990 STM; 1988 PGM) and young regeneration areas (secondary forest after recent, < 10ya, deforestation). Naturally non-forested areas are negligible in both regions. The percentage of mechanized agriculture at the catchment scale was calculated considering annual Moderate Resolution Imaging Spectroradiometer (MODIS) data from 2001 to 2010. Riverscape fragmentation was

estimated by two measures: density of upstream and downstream road crossings in the drainage network, both calculated within a 5 km buffer from the sampling site and scaled by the catchment area. The road crossings were identified by photo interpretation using georeferenced color Rapideye images (2010 for STM and 2011 for PGM, 5 m resolution). Hydrological distance between each sample site and the main river downstream (4th order reaches) were calculated using Landsat images. All landscape analyses were carried out using ArcGis 9.3 (Environmental Systems Research Institute, Redlands, CA, USA). See detailed methodology in Gardner et al. (2013).

Instream physical habitat structure

We adapted the field methods of Peck et al. (2006) to characterize instream physical habitat structure. Each 150 m long sample site was subdivided into 10 continuous sections by 11 cross-sectional transects (Appendix A). Before measurements, the site extremities were blocked with nets (5 mm stretched mesh size) to prevent fish from escaping. Section characterization included the quantification of woody debris volume in the channel and 10 longitudinal equidistant measurements of thalweg depth and presence of fine sediments. At each of the 11 transects we estimated the proportion of different substrate types and water-column depth along five equidistant points, and measured bankfull width and depth. Besides the quantification of wood volume, we assessed fish cover at each transect in 10 m long plots inside the stream channel, using semi-quantitative estimates of the areal cover of leaf packs, standing cover (i.e. roots, overhanging vegetation, undercut banks, and boulders), aquatic macrophytes and submerged grassy vegetation. Forest canopy cover above the channel was measured with a convex densiometer at the center of each transect (facing upstream, downstream, left and right margins) and the mean values were used as a proxy for channel shading. We measured temperature with a digital thermometer placed below the water surface in the center of the site. From these field measurements, we calculated combined physical habitat metrics representing complementary attributes of the local instream conditions (based on Kaufmann et al. 1999, 2009, Hughes and Peck 2008).

Fish sampling

Following the physical habitat assessment, three people sampled fish in the entire area of the site for 120 min in an upstream direction. During this procedure, each 15-m section was isolated with block nets. Fishes were collected during daylight hours using seines (6 x 1.5 m, 5 mm mesh) and semi-circular hand nets (0.8 m in diameter, 2 mm mesh). The use of various

equipment and collection techniques was applied to encompass all kinds of microhabitats and fish groups. Specimens were killed in an anesthetic solution (Eugenol) and then fixed in 10% formalin. In the laboratory, all collected fishes were identified to species and counted.

Functional structure of fish assemblages

To evaluate the functional structure of fish assemblages we first conducted an ecomorphological analysis. Using a set of 18 morphological traits, we characterized each species with respect to three key functions: food acquisition, locomotion, and habitat use (adapted from Villéger et al. 2010; Appendix B). We then computed the functional distance between each pair of species for each regional pool (STM and PGM). Some functional traits were not represented by continuous variables, so we used the Gower distance, which allows considering different types of traits while giving the same weight to each of them (Villéger et al. 2008). We then ran a Principal Coordinate Analysis (PCoA) on each functional distance matrix to build a multidimensional functional space using the first four PCoA axes. This number of dimensions was as a trade-off between computation time and quality of the functional space (i.e., Mantel correlations between the original distance and the Euclidean distance in the functional space: $r = 0.92$ (STM) and 0.88 (PGM)). This choice led us to remove the five STM sites with fewer than five species because of the obligation of having a higher number of species than traits to compute local functional diversity (Villéger et al. 2008).

We used complementary indices to quantitatively describe the functional structure of fish assemblages: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional specialization (FSpe), functional originality (FOri), and community-weighted mean of a trait (CWM). FRic is the amount of functional space filled by all species within the assemblage, indicating the range of trait combinations or niche occupation (i.e., convex hull volume; Villéger et al. 2008). We standardized FRic values for each assemblage by expressing them as a percentage of the volume filled by the pool of species in the respective region. FEve measures the regularity of distribution of abundance in the functional space, and is constrained between 0 and 1, increasing when abundances are more evenly distributed in the functional space (Villéger et al. 2008). FDiv quantifies how the species abundances diverge from the center of the volume filled by the assemblage in the functional space, and ranges between 0 and 1, approaching unity when highly abundant species are very distant from the assemblage center (Villéger et al. 2008). FSpe represents the distinctiveness

of species functional traits in the assemblage (Bellwood et al. 2006), and is expressed as the mean distance between each species and the average position of all species in the functional space (i.e., barycenter of the regional pool of species). FSpe is complementary to FDiv because it depends on the positions of species relative to the barycenter calculated from the regional pool, while FDiv relies only on the functional structure of the target assemblage (Villéger et al. 2010). FOri reflects the degree of uniqueness (i.e., the opposite of redundancy) of species traits in the assemblage (Mouillot et al. 2013), and is expressed as the mean distance between each species and its nearest neighbor in the functional space. The raw values of FSpe and FOri were standardized between 0 and 1 by dividing them, respectively, by the maximum distance to the barycenter and by the maximum nearest-neighbor distance observed over all species present in each region (Mouillot et al. 2013). CWM indicates the functional identity of an assemblage (Lavorel et al. 2008), being expressed as the abundance-weighted average value for each trait (in this study, each PCoA axis). The computations of all functional indices were carried out using the *cluster*, *ape*, and *geometry* packages in R (R Core Team 2014).

Data analyses

To evaluate potential causal pathways of land use on the functional structure of fish assemblages we performed structural equation modeling (SEM). SEM is a statistical framework that deals with simultaneous functioning of multiple processes, contributing to a system-level understanding (Shipley 2000). It is based on the study of theoretically justified models that are parameterized by finding a solution minimizing the difference between the model-implied and the observed data (Riseng et al. 2011). Among the main advantages, Grace et al. (2009) highlighted the ability of SEM applications: to detect relationships through mediating variables; to describe general processes and underlying ecological mechanisms using path coefficients (i.e., regression slopes) and path diagrams; and to obtain information that can be used to predict future outcomes. SEM is sensitive to small sample sizes relative to the number of parameters to be estimated (Grace 2008). Given this limitation, we reduced the original number of variables to reach a better estimation of parameters and increasing the power of analysis. We first carefully chose the set of landscape and instream habitat metrics based on personal knowledge and on related previous studies (e.g., Allan et al. 1997, Allan 2004, Riseng et al. 2011, Casatti et al. 2012). After this, we removed variables taking into account a trade-off between ecological relevance and high statistical correlations. The remaining set of variables included: four land cover and two fragmentation predictors; two

natural landscape predictors; 10 instream habitat variables; two taxonomic and nine functional structure indicators for the fish assemblages (Fig. 2).

We hypothesized that land use acted mostly indirectly on the structure of fish assemblages, mediated by the influences of proximal instream habitat conditions (Fig. 2). Stream bankfull channels are expected to widen (increase in width/depth ratio; BFWD_RATIO), whereas relative residual depth (D_{res}/D_{th} ; a measure of bottom complexity according to Kaufmann and Faustini 2012), relative bed stability (LRBS), and water-column depth (DEPTH) are expected to decrease with increasing deforestation at the local, network and catchment scale, intensification of mechanized agriculture, and fragmentation of the drainage network by upstream road crossings. We hypothesized these pathways because those landscape disturbances tend to increase flood frequency, and erosional-sedimentation processes across the streams (Allan et al. 1997, Kaufmann et al. 2009). We also expected that deforestation at all spatial scales should decrease the amount of wood (WOOD) and coarse litter (LITTER) delivery to, and retained in the stream channel. Deforestation at the local riparian scale is expected to decrease standing cover (STCOV) and shading (SHADE) over the channel which, in turn, should increase water temperature (TEMP) and macrophyte+grass cover (MAGR). Water temperatures should also increase with increasing deforestation at catchment and network riparian scales because of the loss of the regional climatic attenuation promoted by forests. Macrophyte+grass cover should also increase with increasing levels of mechanized agriculture in the catchment that likely augments nutrient inputs and their movement to the streams. Finally, we expect that these multiple instream changes (environmental homogenization and alterations to or loss of natural habitats) should lead to changes in the structure of fish assemblages.

Downstream road crossings were used as an indication of riverscape fragmentation directly influencing local assemblages (Fig. 2) by potentially impairing dispersal of organisms from the rest of the basin downstream from the sample site. We have not considered a direct effect of upstream fragmentation on fish dispersal because headwaters are not expected to act as fish species sources at the microbasin scale (i.e., there is an additive pattern of species richness along the longitudinal continuum; Matthews 1998). Catchment area and distance to large rivers were used as natural landscape predictors of the structure of fish assemblages (Fig. 2), representing, respectively, the natural size and the isolation of each site (i.e., considering the potential importance of fish colonization from larger rivers).

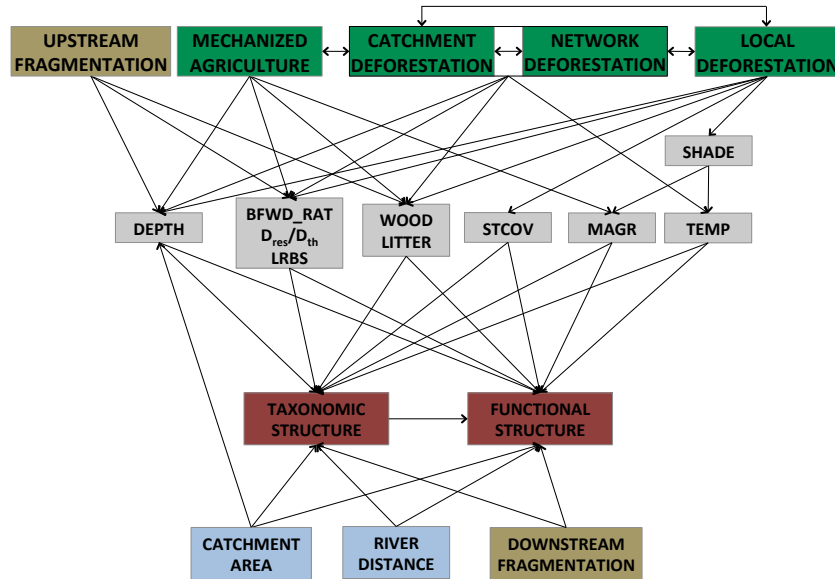


FIG. 2. Hypothesized model tested using Structural Equation Modeling, indicating the expected pathways (arrows) for the effects of land cover (green boxes) and riverscape fragmentation (brown boxes) on the structure of Amazon stream fish assemblages (red boxes). These effects can be direct or indirect, mediated by instream habitat conditions (gray boxes). Natural landscape factors were also considered (blue boxes). Bidirectional arrows indicate expected correlations. DEPTH: water-column depth; BFWD_RAT: bankfull width/depth ratio; D_{res}/D_{th} : relative residual depth (i.e., bottom complexity); LRBS: \log_{10} relative bed stability; WOOD: wood volume; LITTER: coarse litter cover; STCOV: standing cover; SHADE: shading over the channel by forest canopy; MAGR: macrophyte+grass cover; TEMP: water temperature.

Given the expected correlation of some functional indices with the taxonomic structure of assemblages (Villéger et al. 2008), we included species richness (affecting FRic) and the evenness of abundance distribution among species (Pielou index; affecting FEve) in the model. This ultimately would provide a causal framework linking environmental gradients with the functional structure of assemblages directly and indirectly, via taxonomic structure (Fig. 2).

Linearity among variables was assessed by inspection of dispersion plots, and transformations ($\ln(x+1)$ or $\arcsin(\sqrt{x})$) were used when necessary. We tested individual-variable and multivariate normality using, respectively, Shapiro-Wilk's and Mardia's test. Even after transforming several variables, normality was not attained for some of them. Therefore, we used "Bollen-Stine" bootstrap (1000 draws) to evaluate the overall fit of the models. This is a modification of the chi-square statistic that is considered robust to non-normal data distributions (Bollen and Stine 1992), and measures the correspondence between the model

and the observed data structure (i.e., no significance difference, $p > 0.05$, indicates good fitting). All SEM procedures were carried out using the *lavaan* package in R (R Core Team 2014).

RESULTS

Landscape and habitat characteristics

Our sampling design captured a broad gradient of land use, particularly for the proportion of deforestation, which ranged from 0 to *c.* 100% at both local and network riparian scales in both regions (Table 1). We also captured high variability of instream characteristics among sites. For example, the bankfull width/depth ratio ranged from 0.8 (deep and narrow) to *c.* 86.0 (very shallow and wide) in STM. Coarse litter covered from 0 to 95% of the stream bottom in STM; and the proportion of macrophyte+grass ranged from 0 to 76% in PGM sites (Table 1).

Ichthyofauna

We caught a total of 25,132 fish specimens (STM = 6,634; PGM = 18,498) and a total of 141 species (STM = 67; PGM = 112), representing 27 families (STM = 22; PGM = 26), and seven orders (Appendix C). The STM and PGM sites supported averages of 11 (6 to 20) and 23 (6 to 44) species, respectively. Characiformes accounted for the vast majority of captured individuals in both regions (STM = 79.5%; PGM = 83.2%), mainly Characidae, and particularly small-bodied species of *Hyphessobrycon*, *Hemigrammus*, and *Moenkhausia*. Characiformes were also the dominant order in terms of species richness (STM = 46.3%; PGM = 47.3%), followed by Siluriformes (STM = 17.9%; PGM = 27.7%) and Perciformes (STM = 17.9%; PGM = 8.9%). Despite this regional pattern of dominance, the mean taxonomic evenness within sites was relatively high in both regions ($J = 0.66$), ranging from 0.20 to 0.86 in STM and from 0.29 to 0.93 in PGM. The species composition was very different between STM and PGM, with only 27% of the species occurring in both regions (Appendix A). On the other hand, the functional structure of the two regions was highly overlapping, with the PGM species pool encompassing most of the functional diversity found in STM (Appendix A).

TABLE 1. Mean and range (minimum – maximum) of the landscape and instream physical habitat variables used in the Structural Equation Model from Santarém (n = 40) and Paragominas (n = 49) sites.

Variable	Code	Unit	SANTAREM			PARAGOMINAS		
			MEAN	MIN	MAX	MEAN	MIN	MAX
Catchment area	-	ha	2741.26	83.02	22725.98	1251.02	44.30	5045.32
Distance to large river	-	m	5614.36	304.51	17465.63	4741.49	50.12	19780.90
Catchment deforestation	-	%	29.33	0.00	70.08	31.63	0.00	97.26
Network riparian deforestation	-	%	35.32	0.00	100.00	37.78	0.00	95.93
Local riparian deforestation	-	%	35.22	0.00	92.00	62.81	0.00	100.00
Mechanized agriculture	-	%	7.08	0.00	59.45	2.63	0.00	44.04
Upstream road crossings	-	nbr/ha 10 ⁻³	2.05	0.00	12.05	3.06	0.00	22.57
Downstream road crossings	-	nbr/ha 10 ⁻³	0.65	0.00	5.37	2.07	0.00	45.15
Mean water-column depth	DEPTH	mm	37.79	9.38	99.18	40.22	11.62	78.48
Bankfull width/depth ratio	BFWD_RAT	m/m	18.20	0.81	85.95	8.06	2.68	38.62
Relative residual depth	D _{res} /D _{th}	m/m	0.41	0.01	0.83	0.45	0.27	0.73
Relative bed stability	LRBS	log ₁₀ (mm/mm)	-2.30	-3.48	0.14	-1.71	-3.02	0.29
Wood volume	WOOD	mm ³ /m ²	1.61	0.00	10.54	3.18	0.00	14.28
Coarse litter cover	LITTER	%	23.30	0.00	95.24	16.70	0.00	64.76
Standing cover	STCOV	%	37.97	1.82	97.95	39.27	5.91	117.05
Channel shading	SHADE	%	80.28	8.16	99.33	65.65	2.67	99.47
Temperature	TEMP	°C	25.08	23.50	27.70	25.59	23.70	29.20
Macrophyte+grass	MAGR	%	5.03	0.00	52.27	13.46	0.00	76.36

Land use effects on fish functional structure

Structural models had good fit for both regions (STM: $\chi^2 = 492.07$, $df = 187$, $p = 0.602$; PGM: $\chi^2 = 429.44$, $df = 187$, $p = 0.673$). Some variables were poorly explained by the model (Table 2), and some standardized path coefficients were not statistically significant. For the sake of simplicity, these variables and coefficients are not shown in Figs. 3 and 5, but they were retained in the model (i.e., we did not re-specify the structural model *a posteriori*). The rankings of explanation coefficients for habitat and biodiversity variables by the model were relatively similar between STM and PGM (Table 2, Appendix A).

TABLE 2. Overall model explanation (R^2 values from the Structural Equation Model) for each habitat metric and biodiversity index for Santarém (STM) and Paragominas (PGM) streams. Order from higher to lower explanation, considering mean R^2 between regions.

Variable	Code	STM	PGM
Functional richness	FRic	0.83	0.80
Taxonomic richness	S	0.83	0.36
Functional identity (PCoA2)	CWM2	0.62	0.56
Functional identity (PCoA3)	CWM3	0.54	0.56
Functional evenness	FEve	0.60	0.35
Functional divergence	FDiv	0.47	0.40
Functional specialization	FSpe	0.56	0.30
Functional identity (PCoA1)	CWM1	0.54	0.32
Macrophyte+grass	MAGR	0.29	0.52
Water-column depth	DEPTH	0.45	0.35
Taxonomic evenness	J	0.33	0.42
Temperature	TEMP	0.22	0.50
Functional identity (PCoA4)	CWM4	0.44	0.22
Functional originality	FOri	0.15	0.46
Channel shading	SHADE	0.21	0.37
Wood volume	WOOD	0.35	0.22
Bankfull width/depth ratio	BFWD_RATIO	0.20	0.22
Coarse litter cover	LITTER	0.30	0.07
Relative bed stability	LRBS	0.21	0.08
Relative residual depth	D_{res}/D_{th}	0.14	0.07
Standing cover	STCOV	0.02	0.01

Santarém sites

Riverscape fragmentation by upstream road crossings reduced water-column depth, bed stability and bottom complexity of the Santarém sites (Fig. 3). The degree of mechanized agriculture within catchments increased the bankfull width/depth ratio. Deforestation at both the catchment and local riparian scales reduced wood volume, whereas only local deforestation negatively affected coarse litter. Local riparian deforestation also decreased channel shading, which, in turn, increased water temperature and macrophyte+grass cover (Fig. 3). Deforestation at the network riparian scale had no significant effect on any habitat metric assessed; and standing covers were not affected by the land use in Santarém (Fig. 3).

The interaction between landscape and site characteristics resulted in significant indirect land use effects on the ichthyofauna. The degree of deforestation at the local scale negatively affected FRic (total effect = -0.30), via species richness (Fig. 3, Table 3). This effect was mediated by reduced bottom complexity and coarse litter in deforested areas, even considering the positive effect of macrophyte+grass cover on species richness (Fig. 3, Table 3). The total effect of local riparian deforestation on FEve was negative (Table 3), because FEve decreased both with increased macrophyte+grass cover and reduced bottom complexity. Also mediated by reduced bottom complexity, FEve was slightly reduced by upstream fragmentation (Table 3). Conversely, upstream fragmentation increased FSpe, mediated by

reduced bed stability (Fig. 3, Table 3). Riverscape fragmentation by downstream road crossings remarkably influenced several assemblage structure indicators, negatively affecting FRic (either directly or via taxonomic richness), FEve and FDiv (Fig. 3, Table 3). FRic increased (completely via species richness) with catchment area and decreased with distance to the main river. Taxonomic evenness did not predict FEve. FOr was not affected by land use in Santarém.

The structural model also detected effects of land use on fish assemblage functional identity (i.e. the abundance-weighted average value, CWM1–4, for each of the four PCoA axes). Mediated by reduced bottom complexity and bed stability, local riparian deforestation and upstream fragmentation indirectly reduced CWM1, whereas downstream fragmentation increased CWM1 (Fig. 3, Table 1). Catchment area had direct and indirect negative effects, via water-column depth, on CWM1. Species with high scores for PCoA1 (i.e., positively weighting CWM1) have morphological traits that facilitate occupation of the stream bottom and/or highly structured microhabitats (e.g., oral gape wider than deeper and positioned at the lower portion of the head, eyes positioned at the upper portion of the head, numerous viliform or conical teeth; Fig. 4), whereas species with low scores for PCoA1 have morphological traits related to the occupation of mid and upper layers of the water column (e.g., superior oral gape, increased caudal fin-peduncle depth ratio, elongated pectoral fin, crescent-shaped caudal fin, and large laterally positioned eyes; Fig. 4). Downstream fragmentation strongly decreased CWM2, whereas deforestation at both local and catchment scales increased CWM2, mediated by reduced wood volume in the site (Fig. 3, Table 3). Species with low PCoA2 scores have well-developed pectoral fins (Fig. 4), a trait usually present in species with high maneuverability in structured microhabitats; on the other hand, most species with high PCoA2 scores lacked a caudal fin (e.g., Synbranchiformes and most Gymnotiformes), indicating lower propulsion and acceleration efficiency when facing hydrodynamic flows. CWM3 was positively affected by downstream and upstream fragmentation (Fig. 3, Table 3), and positively weighted by fishes with depressed-bodies (high scores for PCoA3; Fig. 4). Conversely, CWM4 was negatively affected by downstream and upstream fragmentation (Fig. 3, Table 3), and positively weighted by large, elongated-body carnivorous fishes (high body mass, low body transversal surface and predominantly canine teeth; Fig. 4).

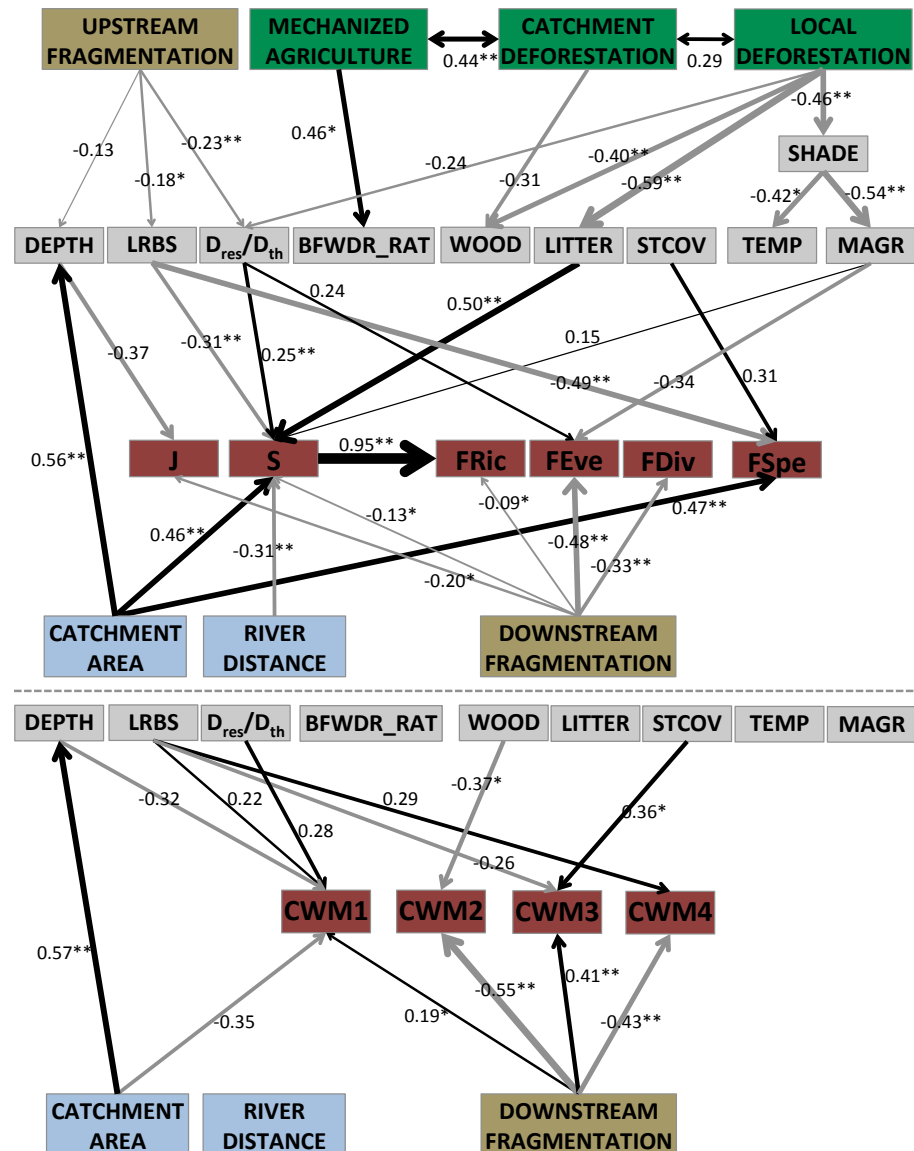


FIG. 3. Structural Equation Model diagram showing the effects of land cover (green boxes), riverscape fragmentation (brown boxes), instream habitat characteristics (gray boxes) and natural landscape factors (blue boxes) on the structure of stream fish assemblages in Santarém region (n=40). Taxonomic structure is represented by species richness (S) and evenness (J). Functional structure is represented by functional richness (FRic), evenness (FEve), divergence (FDiv), specialization (FSpe), and identity (CWM1-4). Unidirectional arrows indicate positive (black) and negative (gray) significant direct effects ($p < 0.10$; * $p < 0.05$; ** $p < 0.01$), with thickness proportional to their power (standardized path coefficients along arrows). Bidirectional arrows indicate significant correlations. Figure divided in two diagrams for the sake of simplicity. DEPTH: water-column depth; BFWDR_RAT: bankfull width/depth ratio; D_{res}/D_{th} : relative residual depth (i.e., bottom complexity); LRBS: \log_{10} relative bed stability; WOOD: wood volume; LITTER: coarse litter cover; STCOV: standing cover; SHADE: shading over the channel by forest canopy; MAGR: macrophyte+grass cover; TEMP: water temperature.

TABLE 3. Total and indirect effects (mediated by instream conditions) of land use on the structure of stream fish assemblages in Santarém (n=40). S: taxonomic richness; J: taxonomic evenness; FRic: functional richness; FEve: Functional evenness; FDiv: Functional divergence; FSpe: Functional specialization; CWM1-4: Functional identity. Only significant path coefficients from the Structural Equation Model are included.

Variable	S	J	FRic	FEve	FDiv	FSpe	CWM1	CWM2	CWM3	CWM4
Local riparian deforestation	-0.32	-	-0.30	-0.14	-	-	-0.07	0.15	-	-
Relative residual depth	-0.06	-	-	-0.06	-	-	-0.07	-	-	-
Wood volume	-	-	-	-	-	-	-	0.15	-	-
Corase litter	-0.29	-	-	-	-	-	-	-	-	-
Macrophyte+grass	0.04	-	-	-0.08	-	-	-	-	-	-
Species richness	-	-	-0.30	-	-	-	-	-	-	-
Catchment deforestation	-	-	-	-	-	-	-	0.11	-	-
Wood volume	-	-	-	-	-	-	-	0.11	-	-
Upstream fragmentation	0.00	0.05	0.00	-0.06	-	0.09	-0.06	-	0.05	-0.05
Water-column depth	-	0.05	-	-	-	-	0.04	-	-	-
Relative bed stability	0.06	-	-	-	-	0.09	-0.04	-	0.05	-0.05
Relative residual depth	-0.06	-	-	-0.06	-	-	-0.06	-	-	-
Species richness	-	-	0.00	-	-	-	-	-	-	-
Downstream fragmentation	-0.13	-0.20	-0.22	-0.48	-0.33	-	0.19	-0.55	0.40	-0.43
Downstream fragmentation*	-0.13	-0.20	-0.09	-0.48	-0.33	-	0.19	-0.55	0.40	-0.43
Species richness	-	-	-0.13	-	-	-	-	-	-	-
Catchment area	0.46	-0.21	0.44	-	-	0.47	-0.53	-	-	-
Catchment area*	0.46	-	-	-	-	0.47	-0.35	-	-	-
Water-column depth	-	-0.21	-	-	-	-	-0.18	-	-	-
Species richness	-	-	0.44	-	-	-	-	-	-	-
River distance	-0.31	-	-0.30	-	-	-	-	-	-	-
River distance*	-0.31	-	-	-	-	-	-	-	-	-
Species richness	-	-	-0.30	-	-	-	-	-	-	-

Note: boldface type in gray rows indicates total effects.

* Direct effect of landscape on fish assemblage structure

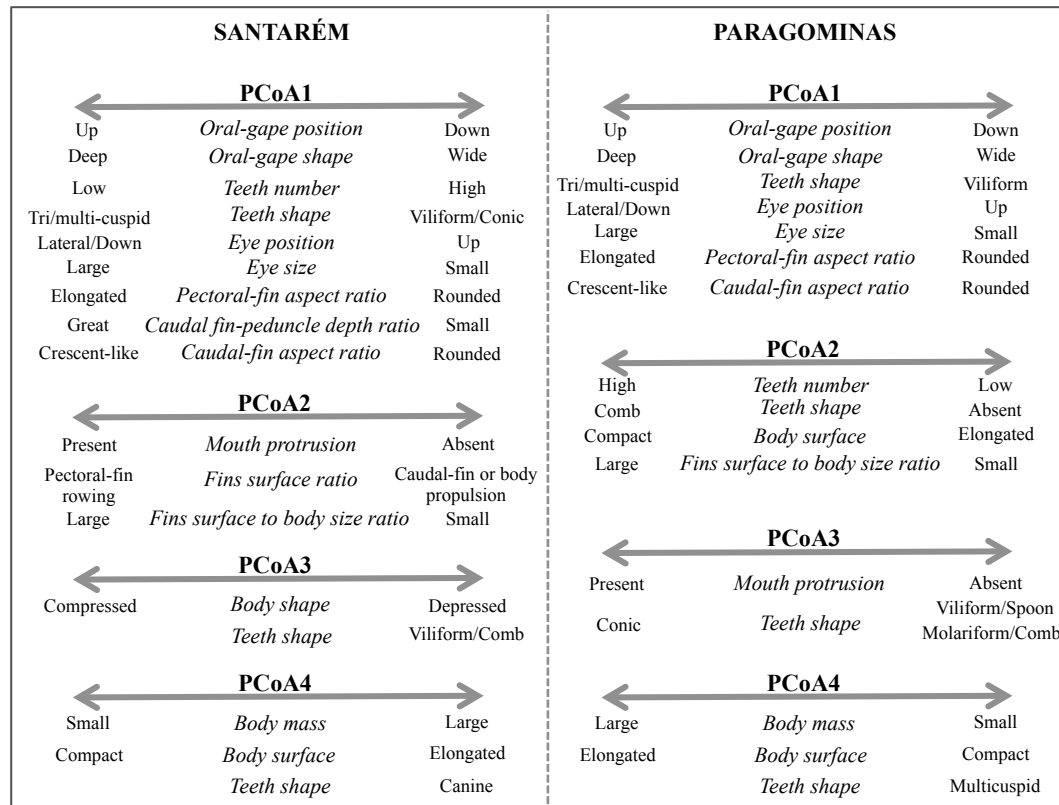


FIG. 4. Position of the predominant state of each ecomorphological trait along each Principal Coordinate (PCoA) axis that composes the multidimensional functional spaces for fish species pools in Santarém (left) and Paragominas (right) sites. The assemblage functional identity (CWM) is the abundance-weighted average value for each of these PCoA axes. See details in Appendix A.

Paragominas sites

Deforestation at the catchment scale strongly increased water temperature, and decreased bed stability and wood volume in the sites (Fig. 5). On the other hand, deforestation at the network riparian scale was associated with increased wood volume. Local riparian deforestation increased the bankfull width/depth ratio, and decreased wood volume and channel shading – increasing water temperature and macrophyte+grass cover (Fig. 5). Upstream fragmentation increased the bankfull width/depth ratio. Mechanized agriculture had no significant effect on any habitat metric assessed. Although influencing different facets of biodiversity, water-column depth, bottom complexity, coarse litter, and standing cover were not significantly affected by land use in Paragominas (Fig. 5).

The degree of deforestation at the catchment and the local riparian scales positively affected FRic, via species richness, while network riparian deforestation negatively affected FRic. The negative relation between wood volume and species richness mediated these effects (Fig. 5,

Table 4). As in Santarem, the total effect of local riparian deforestation on FEve was negative, and FEve decreased with increased macrophyte+grass cover. FSpe was positively affected by deforestation at both catchment and local scales, mediated by the increase in water temperature. FOri was only slightly affected by local riparian deforestation, because the negative impact mediated by macrophyte+grass cover was offset by the positive impact mediated by reduced wood volume. Given its negative relation with wood volume, FOri was positively affected by catchment deforestation but negatively affected by network riparian deforestation (Fig. 5, Table 4). FDiv was affected by the distance to large rivers (positively) and catchment area (negatively). These natural landscape factors did not predict species richness and FRic in Paragominas.

Regarding the influences of land use on the functional identity of the assemblages, network riparian deforestation had a negative total effect on CWM1, mediated by the negative relation with wood volume. For local and catchment scales, this mediated effect was offset by the negative influence of water temperature on CWM1 (Fig. 5, Table 4). CWM1 was positively weighted by species with oral gape wider than deeper and positioned at the lower portion of the head, small eyes positioned at the upper portion of the head, viliform teeth, and rounded pectoral and caudal fins (Fig. 4). CWM2, positively weighted by elongated-body species without (or poorly developed) fins, and negatively weighted by compact-body species with well-developed fins (Fig. 4), was positively affected by downstream fragmentation. CWM2 was negatively affected by upstream fragmentation and local riparian deforestation, both mediated by the negative relation with bankfull width/depth ratio (Fig. 5, Table 4). CWM3, positively weighted by species with viliform, molariform, comb- or spoon-shaped teeth, was positively affected by network riparian deforestation and negatively affected by catchment deforestation (Figs. 4 and 5, Table 4). The positive relation of wood volume with CWM3 mediated these effects. Local riparian deforestation had a small total effect on CWM3, because macrophyte+grass cover offset the influence of wood volume (Fig. 5, Table 4). CWM4, negatively weighted by large elongated-body species, was significantly affected only by catchment area (Figs. 4 and 5, Table 4).

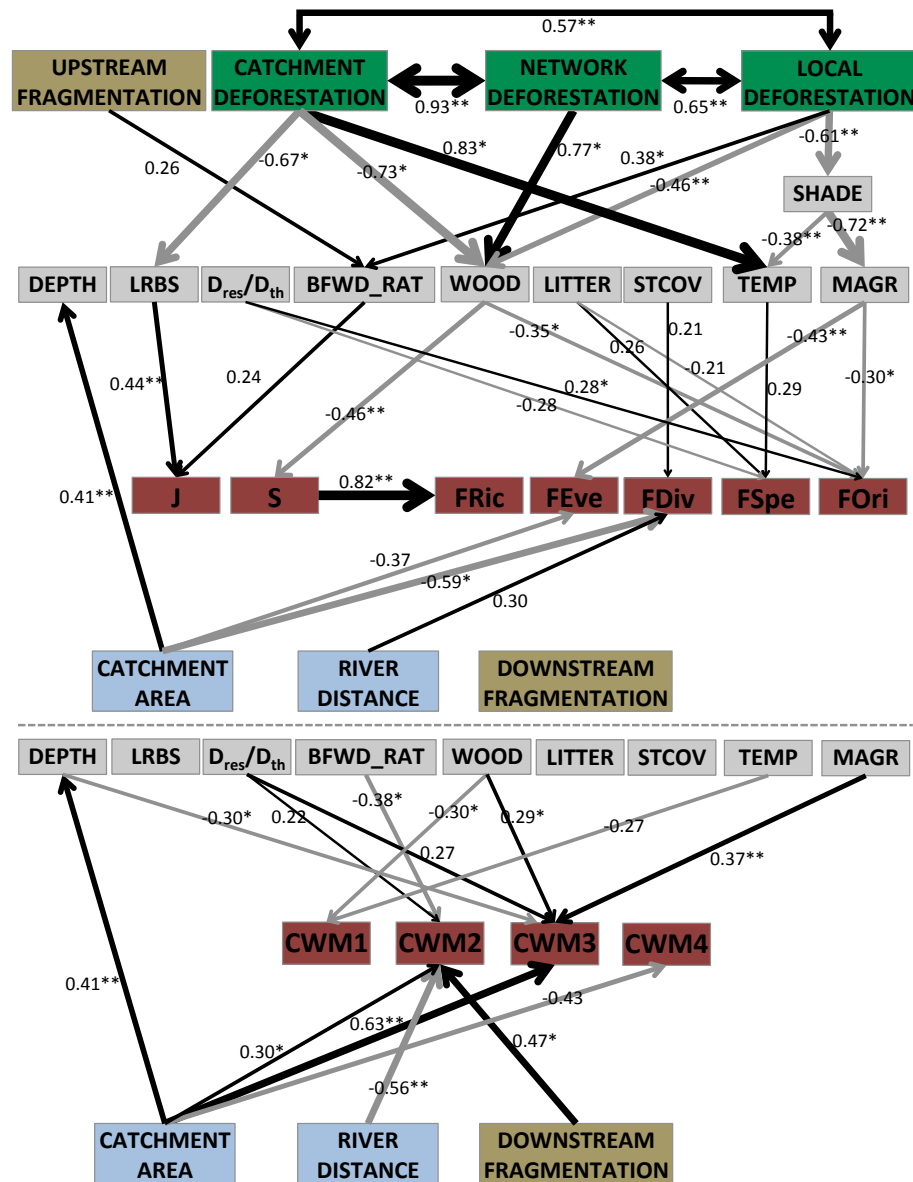


FIG. 5. Structural Equation Model diagram showing the effects of land cover (green boxes), riverscape fragmentation (brown boxes), instream habitat characteristics (gray boxes) and natural landscape factors (blue boxes) on the structure of stream fish assemblages in Paragominas region (n=49). Taxonomic structure is represented by species richness (S) and evenness (J). Functional structure is represented by functional richness (FRic), evenness (FEve), divergence (FDiv), specialization (FSpe), originality (FOri) and identity (CWM1-4). Unidirectional arrows indicate positive (black) and negative (gray) significant direct effects ($p < 0.10$; * $p < 0.05$; ** $p < 0.01$), with thickness proportional to their power (standardized path coefficients along arrows). Bidirectional arrows indicate significant correlations. Figure divided in two diagrams for the sake of simplicity. DEPTH: water-column depth; BFWD_RAT: bankfull width/depth ratio; D_{res}/D_{th} : relative residual depth (i.e., bottom complexity); LRBS: \log_{10} relative bed stability; WOOD: wood volume; LITTER: coarse litter cover; STCOV: standing cover; SHADE: shading over the channel by forest canopy; MAGR: macrophyte+grass cover; TEMP: water temperature.

TABLE 4. Total and indirect effects (mediated by instream conditions) of land use on the structure of stream fish assemblages in Paragominas (n=49). S: taxonomic richness; J: taxonomic evenness; FRic: functional richness; FEve: Functional evenness; FDiv: Functional divergence; FSpe: Functional specialization; FOri: Functional originality; CWM1-4: Functional identity. Only significant path coefficients from the Structural Equation Model included.

Variable	S	J	FRic	FEve	FDiv	FSpe	FOri	CWM1	CWM2	CWM3	CWM4
Local riparian deforestation	0.21	0.09	0.17	-0.19	-	0.07	0.03	0.08	-0.14	0.03	-
Bankfull width/depth ratio	-	0.09	-	-	-	-	-	-	-0.14	-	-
Wood volume	0.21	-	-	-	-	-	0.16	0.14	-	-0.13	-
Water temperature	-	-	-	-	-	0.07	-	-0.06	-	-	-
Macrophyte+grass	-	-	-	-0.19	-	-	-0.13	-	-	0.16	-
Species richness	-	-	0.17	-	-	-	-	-	-	-	-
Network riparian deforestation	-0.35	-	-0.29	-	-	-	-0.27	-0.23	-	0.22	-
Wood volume	-0.35	-	-	-	-	-	-0.27	-0.23	-	0.22	-
Species richness	-	-	-0.29	-	-	-	-	-	-	-	-
Catchment deforestation	0.34	-0.30	0.28	-	-	0.24	0.26	0.00	-	-0.21	-
Relative bed stability	-	-0.30	-	-	-	-	-	-	-	-	-
Wood volume	0.34	-	-	-	-	-	0.26	0.22	-	-0.21	-
Water temperature	-	-	-	-	-	0.24	-	-0.23	-	-	-
Species richness	-	-	0.28	-	-	-	-	-	-	-	-
Upstream fragmentation	-	0.06	-	-	-	-	-	-	-0.10	-	-
Bankfull width/depth ratio	-	0.06	-	-	-	-	-	-	-0.10	-	-
Downstream fragmentation	-	-	-	-	-	-	-	-	0.47	-	-
Downstream fragmentation*	-	-	-	-	-	-	-	-	0.47	-	-
Catchment area	-	-	-	-0.37	-0.59	-	-	-	0.30	0.51	-0.43
Catchment area*	-	-	-	-0.37	-0.59	-	-	-	0.30	0.63	-0.43
Water-column depth	-	-	-	-	-	-	-	-	-	-0.12	-
River distance	-	-	-	-	0.30	-	-	-	-0.56	-	-
River distance*	-	-	-	-	0.30	-	-	-	-0.56	-	-

Note: boldface type in gray rows indicates total effects.

* Direct effect of landscape on fish assemblage structure

DISCUSSION

The multifaceted nature of land use effects on habitat and fish assemblage structure in streams is widely recognized (Wang et al. 2001, Allan 2004, Hughes et al. 2006), but the complexity involving these relationships has often limited conclusive and generalized outcomes. This difficulty seems even more acute for small Amazon streams, where the basic knowledge of their natural dynamics and species natural histories are largely lacking (Carvalho et al. 2009). By analysing complementary spatial scales and contrasted intensities of land use, we disentangled the pathways through which deforestation and riverscape fragmentation affect the structure of fish assemblages in these ecosystems. We identified distinct, sometimes inverse, responses to land use between and within different components (i.e., functional and taxonomic) of assemblage structure illustrating the need to consider all possible facets when assessing biodiversity in changing landscapes (Hillebrand et al. 2008, Villéger et al. 2010). Finally, our results suggest that although some disturbance effects through a given pathway

offset others, the combined negative effects of different land use predictors (e.g., local riparian deforestation + road crossings) may represent double jeopardies for stream ichthyofauna.

Land use, instream habitat and the functional structure of assemblages

We found some congruent patterns for streams from the two study regions (Santarém – STM and Paragominas – PGM) when assessing land use effects on fish assemblages mediated by habitat conditions. For instance, local riparian deforestation increased macrophyte+grass cover via decreases in shading over the channel. A shared functional response of this structural change in both regions was the reduced functional evenness (FEve) within assemblages. Therefore, deforestation increased the dominance of a few trait combinations, indicating that the most abundant species in macrophyte+grass dominated streams are functionally similar (i.e., concentrated in a restricted position within the functional space of the assemblages). Particularly for STM, while decreasing FEve this disturbance pathway increased species richness and had no direct effect on functional richness. This suggests that fish assemblages in deforested streams are not functionally poorer but their species traits are more unevenly distributed. Another pathway reducing FEve in STM was through changes in bottom complexity, exacerbating the total negative effect of local riparian deforestation on this functional index. Interestingly, taxonomic evenness was not significantly influenced in these pathways and it did not predict FEve, reinforcing the potential to add important complementary information when assessing biodiversity in its multiple facets.

Decreasing functional evenness may have critical consequences for ecosystem functioning if aggregate community properties are important to ecological processes. For example, the presence of niches unoccupied by the native assemblage can favor invasion by non-natives (Hillebrand et al. 2008). Indeed, non-native species, which are often more tolerant, tend to be more successful in colonizing streams after habitat alterations (Baltz and Moyle 1993, Hughes et al. 2005, Lomnický et al. 2007). Compared with many rivers worldwide, successful invasions of non-native fish within the Amazon Basin are less common (Leprieur et al. 2008). However, the consistent decrease of FEve of fish assemblages along the deforestation gradients assessed herein increases their susceptibility to invasive species introductions, and may be an advanced warning that cascading effects on native assemblages across Amazonian streams may result if non-native introductions occur along with anthropogenic disturbance (Leprieur et al. 2008).

Beyond effects on FEve, the increases in macrophyte+grass cover resulting from local deforestation decreased the functional originality (FOri) of assemblages in PGM streams. In contrast to FEve, which considers species similarity within a local assemblage, FOri is measured based on species similarity at the regional level (Mouillot et al. 2013). The decrease of both these indices thus indicates that the deforestation-induced increase in macrophyte+grass cover increases the functional redundancy of the assemblages, corroborating previous findings that environmental degradation led to replacement of species having unique traits by functionally redundant ones (Ernst et al. 2006, Villéger et al. 2010).

Oposing effects occurred for the functional identity of the assemblages in PGM streams (see CWM3 in Fig. 5). On the one hand, local riparian deforestation negatively affected wood-eating species (e.g., *Hypostomus* cf. *cochliodon*; species with spoon-shaped teeth, high scores for PCoA3), mediated by reductions in site wood volume. On the other hand, this landscape alteration positively affected periphyton-grazer fishes (e.g., *Ancistrus*, *Farlowella*, *Parotocinclus*, *Rineloricaria*; genera with comb-shaped teeth, high scores for PCoA3), mediated by increases in macrophyte+grass cover. Notably, both trophic groups occur in the same family (Loricariidae), which usually was reported as being favored by deforestation (e.g., Bojsen and Barriga 2002). These contrasting effects on the same taxonomic group and by the same landscape predictor illustrate common limitations faced by most investigations of land use on stream communities. In this context, we suggest that further studies should search for the finest possible trait-based information and incorporate it in a functional perspective capable of differentiating properties within taxonomic groups (i.e., not all loricariids are periphyton-grazers). This is particularly critical for species-rich tropical ecosystems, where high levels of niche diversification are likely (Winemiller 1991). These findings also call for the need to explore the mechanistic and simultaneous causal pathways through which disturbances affect stream ecosystems (Riseng et al. 2011), to go further than just examining direct landscape-assemblage relationships.

Although some of the pathways differed between regions, land use altered the channel morphology and the physical structure of stream bottoms. The bankfull width/depth ratio increased with upstream fragmentation and local deforestation in PGM, and with the intensification of mechanized agriculture in STM. Relative bed stability decreased with catchment deforestation in PGM, whereas this metric, water-column depth and bottom

complexity decreased with upstream fragmentation in STM. Regardless of the predominant pathway, the process behind those structural alterations on streams is likely the same: the erosion of exposed soil and subsequent runoff of high amounts of fine sediments into the channel, embedding consolidated structures over the bottom. Sedimentation is known to lead to drastic changes in the structure of fish assemblages, being considered one of the main threats for some functional groups (e.g., lithophilous spawners) in both temperate and tropical streams (Walser and Bart 1999, Sutherland et al. 2002, Casatti et al. 2006, Bryce et al. 2010). We had not expected such severe consequences for lowland regions of the Amazon, where streams are naturally dominated by sand and fines, and are rarely composed of rock substrate. However, the negative relation of bed stability (in STM) and bottom complexity (in PGM) with the functional specialization of the assemblages suggests that only species holding very specific combinations of traits should inhabit unstable bottoms in those streams. Furthermore, our findings suggest which traits related to foraging and habitat preferences should be more responsive in each disturbance pathway. For instance, in STM streams, species with traits associated with the use of the benthic compartment (e.g., oral gape wider than deeper and positioned at the lower portion of the head; eyes positioned at the upper portion of the head) were most affected by reductions in bottom complexity and bed stability. On the other hand, species having morphological traits related to the occupation of mid and upper layers of the water column (e.g., superior oral gape, increased caudal fin-peduncle depth ratio, crescent-shaped caudal fin, and large laterally positioned eyes) were negatively affected by reductions of water-column depth (see CWM1 in Fig. 3). These habitat-species relationships suggest that trait filtering is an important mechanism structuring Amazonian fish assemblages across land use gradients.

Loss of connectivity and the functional structure of assemblages

Land use not only alters local instream habitat conditions, but also impedes movement of organisms throughout river networks (Urban et al. 2006, Perkin and Gido 2012). One of the most remarkable findings in our study was the strong influence of downstream fragmentation on several components of fish assemblage structure in STM. The density of road crossings downstream from sample sites had a direct negative impact on functional richness, which, in addition to the indirect effect via taxonomic richness, indicates that losing regional connectivity potentially reduces the range of niche occupation by local assemblages. Furthermore, this disturbance was negatively correlated with functional evenness and divergence of fish assemblages. This suggests a trend of functional homogenization of local

assemblages, increasing concentration of the most abundant species near the center of assemblage functional space.

These results are likely linked to reduced dispersal of species from larger rivers or of fish groups unable to establish stable local populations in small streams, as indicated by the predominant morphological traits across sites (see CWM1-4 in Fig. 3). For instance, large elongated-body carnivorous/piscivorous species (i.e., high body mass, low body transversal surface, canine teeth; high scores for PCoA4) were strongly negatively correlated with downstream fragmentation in STM streams. Because of the oligotrophic conditions of natural Amazonian streams, these top predators (e.g., *Acestrorhynchus falcatus*, *Hoplias curupira*, *H. malabaricus*) may have to alternate the search for food resources across different microbasins, having greater dependence on spatial connectivity. Given that predation is an important assembly mechanism in streams (Jackson et al. 2001), the loss of these functional entities may result in severe impacts to local communities. Other fish groups vulnerable to local extinctions following riverscape fragmentation are those characterized by body morphologies indicative of weaker swimming ability, which potentially have poor dispersal capability (Olden et al. 2008). This is consistent with our findings, because species with poorly developed fins (high scores for PCoA2) or highly laterally compressed bodies (low scores for PCoA3) were strongly negatively correlated with road crossing density in STM.

Study limitations and general recommendations

We believe this study offers significant insights concerning functional responses of stream fish assemblages to landscape alterations in the Amazon. Nevertheless, we also recognize that it is a starting point, and its limitations suggest fruitful opportunities for future investigations. Firstly, as pointed out by Riseng et al. (2011), structural equation modeling is a simplification of a much more complex reality, meaning that it can only support or contradict causal hypotheses, but cannot prove causation (i.e., like a controlled experiment). However, considering the huge operational difficulties to make direct large-scale experimentation in species-rich regions, we considered SEM as a useful analytical tool for our study. Secondly, even taking into account several landscape and instream habitat predictors, we lack some important field information at the regional scale to increase the power of our explanations. For instance, contrasting with the strong effects in STM streams, fragmentation was a weak predictor of functional changes in PGM fish assemblages, even though the mean density of road crossings were greater in PGM (Table 1). Given that the functional structure of the two

regional assemblages is highly overlapping (i.e., potentially similar dispersal capabilities), we tentatively interpret this result as a reflection of differing permeability of the road crossing. Appropriately constructed bridges often do not represent effective obstacles for stream fishes, whereas passages with highly elevated culvert outlets (frequently observed in STM) may prevent several species from dispersing upstream (Nislow et al. 2011). Therefore, beyond GIS estimates, a thorough assessment of road crossing character and effectiveness of barriers would likely yield more efficient management strategies to reduce stream fragmentation. Finally, although we have used a relatively high number of traits to characterize the species, they were restricted to functions related to food acquisition, locomotion and habitat preferences. Including traits describing fish ecophysiology and reproduction are clearly desirable to better interpret potential critical pathways of disturbances (e.g., increases in water temperature resulting from deforestation). Therefore, filling the wide knowledge gaps in species natural histories should be a priority in the conservation agenda for Amazon stream fishes.

Conclusions

The rapid and intense agricultural development in the tropics is resulting in highly degraded landscapes, and even relatively well-preserved biomes such as the Amazon are severely threatened. This study illustrates how land use, through several pathways and spatial scales, alters the functional structure of fish assemblages in small streams of two regions in the mid-eastern Amazon. It was possible to identify general assemblage indicators (e.g., functional evenness) and specific trait combinations that should be most affected by both deforestation and riverscape fragmentation by road crossings. However, even considering some congruent functional responses to land use, several disturbance pathways were notably different between the two regions. For instance, deforestation at the catchment and the network riparian scales had small influences in the STM model, but these factors had strong weight in PGM. On the other hand, local riparian deforestation and channel fragmentation were key predictors of functional changes in STM assemblages, suggesting that numerous local disturbances widely distributed across watersheds may be damaging to fish assemblages in that region. Therefore, specific strategies of regional management are needed for the effective conservation of stream ichthyofauna. Overall, our findings clearly corroborate the current view in ecology and conservation biology that biodiversity should be assessed in a multifaceted framework that explicitly takes into account the functional elements of biotic assemblages.

ACKNOWLEDGEMENTS

We thank D. Bastos, D. Carvalho, R. Duarte, T. Franco, L. Juen, K. Silva, V. Oliveira, J. Brito, J. Oliveira-Silva, C. Chaves, Miriam, Marcos, L. Brasil, L. Pires, L. Silva, M. Nascimento, R. Freitas, M. Oliveira, for assistance in the field work and the farmers and workers unions of Santarém, Belterra, and Paragominas and all collaborating private landowners for their support. N. Rabelo and S. Cunha helped with fish ecomorphological analysis and A. Dias helped with SEM. J. Grace, F. Teresa, T. Oberdorff, C. Cornelius, S. Amadio, C. Deus revised the manuscript. This work was financially supported by: Instituto Nacional de Ciência e Tecnologia – Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0), Empresa Brasileira de Pesquisa Agropecuária – Embrapa (SEG: 02.08.06.005.00), the UK government Darwin Initiative (17-023), The Nature Conservancy, Natural Environment Research Council (NERC) (NE/F01614X/1 and NE/G000816/1), Fulbright Brasil and Amnis Opes Institute. JZ received a productivity grant from CNPq (#307464/2009-1). JB was supported by CNPq 400640/2012-0. This study is part of RPL PhD thesis, supported by CNPq (#156915/2011-1) and CAPES (Science Without Borders - PDSE #1914-13-8). This is, respectively, the contribution # XX and # XX of the Projeto Igarapés and Rede Amazônia Sustentável publication series.

REFERENCES

- Allan, J. D. 2004. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35:257–284.
- Allan, J. D., D. L. Erickson, and F. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37:149–161.
- Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* 3:246–255.
- Bellwood, D. R., P. C. Wainwright, C. J. Fulton, and A. S. Hoey. 2006. Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B* 273:101–107.
- Bojsen, B. H., and R. Barriga. 2002. Effects of deforestation on fish community structure in Ecuadorian Amazon streams. *Freshwater Biology* 47:2246–2260.

- Bollen, K. A., and R. A. Stine. 1992. Bootstrapping goodness-of-fit measures in structural equation models. *Sociological Methods and Research* 21:205–229.
- Brooks, T. M., R. A. Mittermeier, G. A. B. Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. *Science* 313:58–61.
- Bryce, S. A., G. A. Lomnický, and P. R. Kaufmann. 2010. Protecting sediment-sensitive aquatic species in mountain streams through the application of biologically based sediment criteria. *Journal of the North American Benthological Society* 29: 657–672.
- Casatti, L., F. Langeani, A. M. Silva, and R. M. C. Castro. 2006. Stream fish, water and habitat quality in a pasture dominated basin, southeastern Brazil. *Brazilian Journal of Biology* 66:681–696.
- Casatti, L., F. B. Teresa, T. Gonçalves-Souza, E. Bessa, A. R. Manzotti, C. S. Gonçalves, and J. O. Zeni. 2012. From forests to cattail: how does the riparian zone influence stream fish? *Neotropical Ichthyology*. 10:205–214.
- Castello L., D. G. McGrath, L. L. Hess, M. T. Coe, P. A. Lefebvre, P. Petry, M. N. Macedo, V. F. Renó, and C. C. Arantes. 2013. The vulnerability of Amazon freshwater ecosystems. *Conservation Letters* 6:217–229.
- Carvalho, L. N., J. Zuanon, and I. Sazima. 2009. Natural History of Amazon Fishes. Pages 113–144 in K. Del Claro, P. S. Oliveira, V. Rico-Gray, A. Ramirez, A. A. A. Barbosa, A. Bonet, et al., editors. *Tropical biology and conservation management: case studies*, Eolss Publishers Co. Ltd., Oxford, UK.
- Chapman, L. J., and C. A. Chapman. 2002. Tropical forest degradation and aquatic ecosystems: our current state of knowledge. Pages 237–249 in M. J. Collares-Pereira, I. G. Cowx, and M. M. Coelho, editors. *Conservation of freshwater fishes: options for the future*. Blackwell Science, Oxford, UK.

Ernst, R., K. E. Linsenmair, and M. O. Rodel. 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biological Conservation* 133:143–155.

Espírito-Santo, H. M. V., W. E. Magnusson, J. Zuanon, F. P. Mendonça, and V. L. Landeiro. 2009. Seasonal variation in the composition of fish assemblages in small Amazonian forest streams: evidence for predictable changes. *Freshwater Biology* 54:536–548.

Fausch K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52:483–98.

Ferreira, J., L. E. O. C. Aragão, J. Barlow, P. Barreto, E. Berenguer, M. Bustamante, T. A. Gardner, A. C. Lees, A. Lima, J. Louzada, R. Pardini, L. Parry, C. A. Peres, P. S. Pompeu, M. Tbarelli, and J. Zuanon. 2014. Brazil's environmental leadership at risk: mining and dams threaten protected areas. *Science* 346:706–707.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogueira, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12:22–33.

Frederico, R. G. 2014. Explorando o nicho de peixes de água doce: uma abordagem evolutiva e conservacionista em igrapés de terra firme amazônicos. PhD Thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil.

Gardner, T. A., J. Ferreira, J. Barlow, A. Lees, L. Parry, I. C. G. Vieira, et al. 2013. A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B*. 368:20120166.

Godar, J., T. A. Gardner, J. Tizado, and P. Pacheco. 2014. Actor-specific contributions to the deforestation slowdown in the Brazilian Amazon. *Proceedings of the National Academy of Sciences USA* 111:15591–15596.

Grace, J. B. 2008. Structural equation modeling for observational studies. *Journal of Wildlife Management* 72:14–22.

Grace, J. B., A. Youngblood, and S. M. Scheiner. 2009. Structural Equation Modeling and Ecological Experiments. Pages 19–46 *in* S. Miao, S. Carstenn, and M. Nungesser, editors. *Real World Ecology: large-scale and long-term case studies and methods*. Springer Science, New York, USA.

Hansen, M. C., S. V. Stehman, and P. V. Potapov. 2010. Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences USA* 107:8650–8655.

Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89:1510–1520.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.

Hughes, R. M., and D. V. Peck. 2008. Acquiring data for large aquatic resource surveys: the art of compromise among science, logistics, and reality. *Journal of the North American Benthological Society* 27:837–859.

Hughes, R. M., J. N. Rinne, and B. Calamusso. 2005. Historical changes in large river fish assemblages of the Americas: a synthesis. Pages 603–612 *in* J. N. Rinne, R. M. Hughes, and B. Calamusso, editors. *Historical changes in large river fish assemblages of the Americas*. Symposium 45. American Fisheries Society, Bethesda, MD, USA.

Hughes, R. M., L. Wang, and P. W. Seelbach. 2006. Landscape influences on stream habitat and biological assemblages. Symposium 48, American Fisheries Society, Bethesda, MD, USA.

INPE. 2013. Projeto PRODES: Monitoramento da floresta Amazônica Brasileira por satélite. Available at www.obt.inpe.br/prodes.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157–170.

Johnson, P. T. J., J. T. Hoverman, V. J. McKenzie, A. R. Blaustein, and K. L. D. Richgels. 2013. Urbanization and wetland communities: applying metacommunity theory to understand the local and landscape effects. *Journal of Applied Ecology* 50:34–42.

Kaufmann, P. R., D. P. Larsen, and J. Faustini. 2009. Bed stability and sedimentation associated with human disturbances in pacific northwest streams. *Journal of the American Water Resources Association* 45:434–459.

Kaufmann, P. R., D. P., and J. Faustini. 2012. Simple measures of channel habitat complexity predict transient hydraulic storage in streams. *Hydrobiologia* 685:69–95.

Kaufmann, P. R., P. Levine, E. G. Robison, C. Seeliger, and D. V. Peck. 1999. Quantifying Physical Habitat in Wadeable Streams. EPA/620/R-99/003. U.S. Environmental Protection Agency, Washington, D.C., USA.

Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, et al. 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology* 22:134–147.

Leprieur, F., O. Beauchard, S. Blanchet, T. Oberdorff, and S. Brosse. 2008. Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology* 6(2): e28. doi:10.1371/journal.pbio.0060028

Limburg, K. E., R. M. Hughes, D. C. Jackson, and B. Czech. 2011. Population increase, economic growth, and fish conservation: collision course or savvy stewardship? *Fisheries* 36:27–35.

Lomnický, G. A., T. R. Whittier, R. M. Hughes, and D. V. Peck. 2007. Distribution of nonnative aquatic vertebrates in western U.S. streams and rivers. *North American Journal of*

Fisheries Management 27:1082–1093.

Lorion, C. M., and B. P. Kennedy. 2009. Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams. *Ecological Applications* 19: 468–479.

Lyons J., S. Navarro-Pérez, P. A. Cochran, E. Santana, and M. Guzmán-Arroyo. 1995. Index of biotic integrity based on fish assemblages for the conservation of streams and rivers in west-central Mexico. *Conservation Biology* 9:569–584.

Mantyka-Pringle, C., T. G. Martin, D. B. Moffatt, S. Linke, and J. R. Rhodes. 2014. Understanding and predicting the combined effects of climate change and land-use change on freshwater macroinvertebrates and fish. *Journal of Applied Ecology* 51:572–581.

Marzin, A. P., P. Verdonschot, and D. Pont. 2012. The relative influence of catchment, riparian corridor and local anthropogenic pressures on fish and macroinvertebrate assemblages in French rivers. *Hydrobiologia* 704: 375–388.

Matthews, W. J. 1998. *Patterns in freshwater fish ecology*. Chapman and Hall, New York, USA.

Mendonça, F. P., W. E. Magnusson, and J. Zuanon. 2005. Relationships Between Habitat Characteristics and Fish Assemblages in Small Streams of Central Amazonia. *Copeia* 4:750–763.

Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28:167–177.

Mouillot, D., S. Villéger, M. Scherer-Lorenzen, and N. W. H. Mason. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* 6:e17476.

Nislow, K. H., M. Hudy, B. H. Letcher, and E. P. Smith. 2011. Variation in local abundance

and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. *Freshwater Biology* 56: 2135–2144.

Nunes, S. S., J. Barlow, T. A. Gardner, J. V. Siqueira, M. R. Sales, and C. M. Souza Jr. 2014. A 22 year assessment of deforestation and restoration in riparian forests in the eastern Brazilian Amazon. *Environmental Conservation* DOI:10.1017/S0376892914000356.

Olden, J. D., N. L. Poff, and K. R. Bestgen. 2008. Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology* 89:847–856.

Peck, D. V., A. T. Herlihy, B. H. Hill, R. M. Hughes, P. R., Kaufmann, D. J. Klemm, et al. 2006. Environmental Monitoring and Assessment Program: Surface Waters Western Pilot Study – field operations manual for wadeable streams. EPA620/R-06/003. U.S. Environmental Protection Agency, Washington, DC, USA.

Perkin, J. S., and K. Gido. 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecological Applications* 22:2176–2187.

Petchey, O. L., A. Hector, and K. J. Gaston. 2004. How do different measures of functional diversity perform? *Ecology* 85:847–857.

R Core Team 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at: [http:// www.R-project.org](http://www.R-project.org). Last accessed 19 December 2014.

Riseng, C. M., M. J. Wiley, R. W. Black, and D. Munn. 2011. Impacts of agricultural land use on biological integrity: a causal analysis. *Ecological Applications* 21:3128–3146.

Roth, N. E., J. D. Allan, D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* 11:141–56

Shipley, B. 2000. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge, UK.

Soares-Filho, B., R. Rajão, M. Macedo, A. Carneiro, W. Costa, M. Coe, et al. 2014. Cracking Brazil's Forest Code. *Science* 344:363–364.

Sutherland, A. B., J. L. Mayer, and E. P. Gardiner. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology* 47:1791–1805.

Teresa F. B., and L. Casatti. 2012. Influence of forest cover and mesohabitat types on functional and taxonomic diversity of fish communities in Neotropical lowland streams. *Ecology of Freshwater Fish* 21:433–442.

Terra, B. D. F., R. M. Hughes, and F. G. Araujo. *In press*. Fish assemblages in Atlantic Forest streams: the relative influence of local and catchment environments on taxonomic and functional species. *Ecology of Freshwater Fish*.

Urban, M. C., D. K. Skelly, D. Burchsted, W. Price, and S. Lowry. 2006. Stream communities across a rural-urban landscape gradient. *Diversity and Distributions* 12:337–350.

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.

Villéger, S., J. R. Miranda, D. F. Hernandez, and D. Mouillot. 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20:1512–1522.

Walser, C. A., and H. L. Bart. 1999. Influence of agriculture on instream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River System. *Ecology of Freshwater Fish* 8:237–246.

Wang, L., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management* 28:255–266.

Whittier, T.R., J.L. Stoddard, R.M. Hughes, and G. Lomnický. 2006. Associations among catchment- and site-scale disturbance indicators and biological assemblages at least- and

most-disturbed stream and river sites in the western USA. Pages 641–664 *in* R.M. Hughes, L. Wang, and P.W. Seelbach, editors. Landscape influences on stream habitat and biological assemblages. Symposium 48, American Fisheries Society, Bethesda, MD, USA.

Winemiller, K. O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs* 61: 343–365.

SUPPORTING INFORMATION

Disentangling the multiple effects of land use on the functional structure of fish assemblages in Amazon streams

APPENDIX A

Supplementary figures

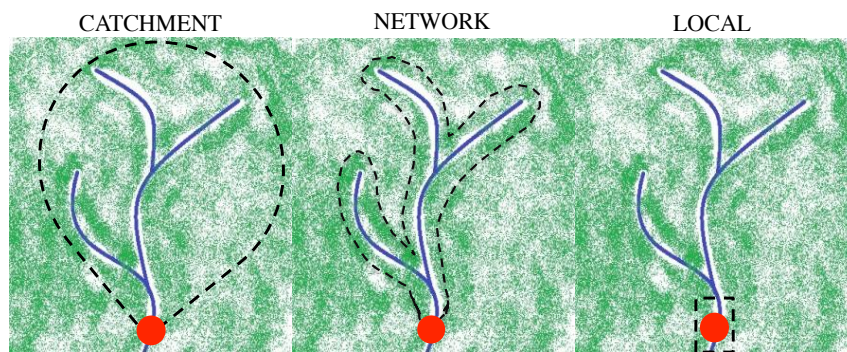


FIG. S1. Representation of the three different spatial scales (dashed lines) assessed for landscape analyses: the whole catchment upstream from sample site (“catchment”); 100-m wide buffer along the entire drainage network upstream from sample site (“network riparian”), and 100-m wide buffer around the sampled site (“local riparian”). Sample site is a 150-m long stream reach (red dot).

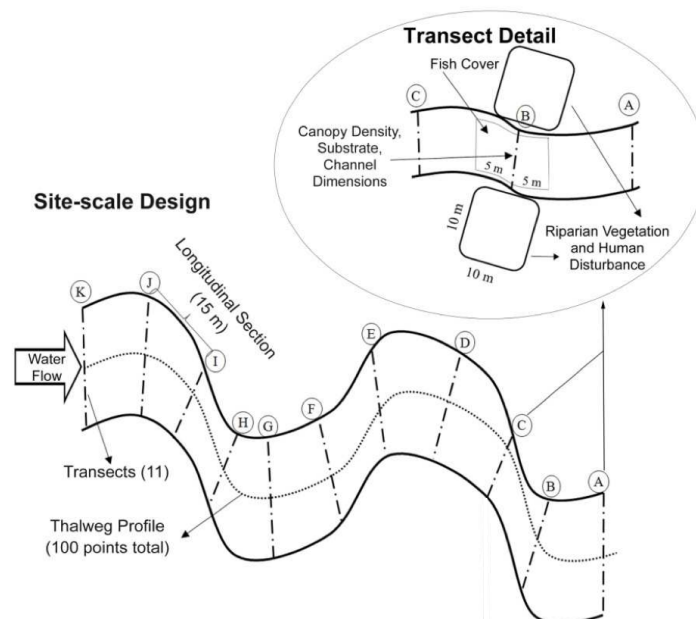


FIG. S2. Schematic representation of the sampled stream stretch. Each transect was named from the downstream (“A”) to upstream (“K”) and marked with flags along the stream stretch. A total of 11 transects and 10 longitudinal sections of 15m were established.

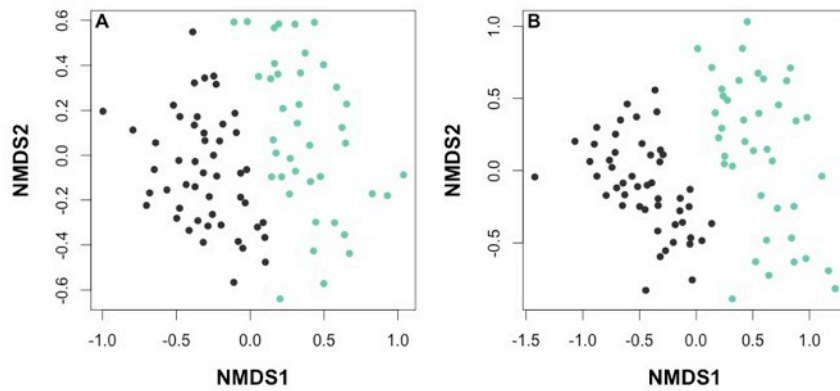


FIG. S3. Non-metric Multidimensional Scaling (NMDS) ordination of sites from Santarém ($n = 40$; green dots) and from Paragominas ($n = 49$; dark gray dots) based on fish species abundance (A) and presence/absence within streams (B).

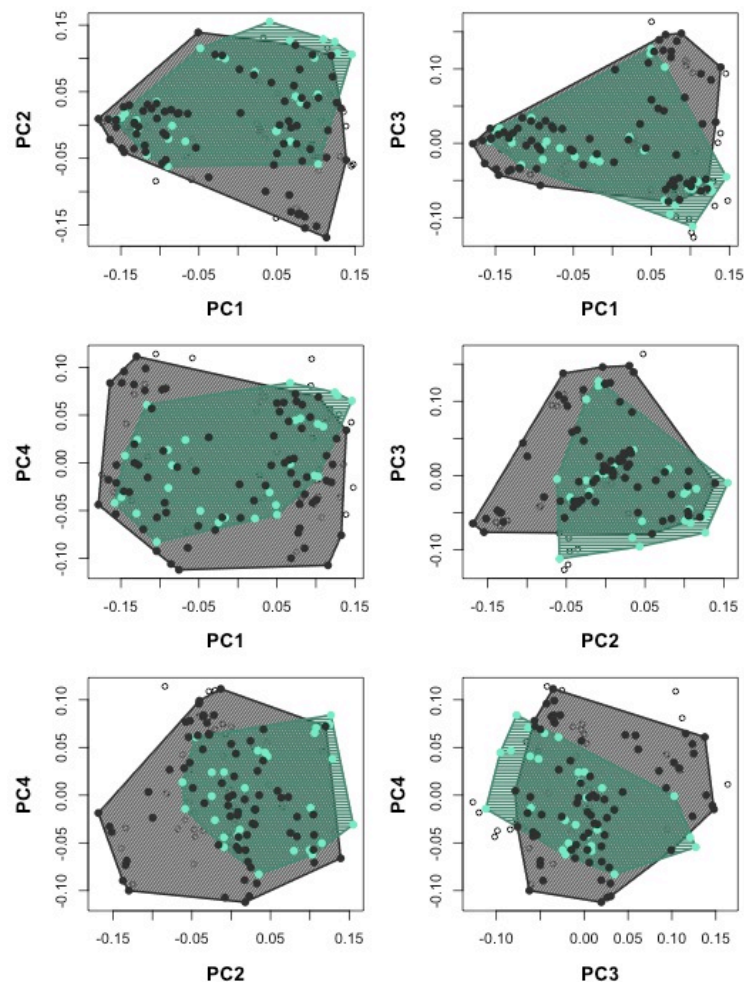


FIG. S4. Four-dimensional representation of the functional space of the global pool (141 species) of stream fishes from Santarém and Paragominas, mid-eastern Amazon basin. Each plot represents two axes of a Principal Coordinate Analysis (PC), where species are plotted according to their respective trait values. Species occurring in both regions are represented by empty circles. Species found exclusively in Santarém or exclusively in Paragominas are filled with green and dark gray, respectively. Projections of the convex hull volumes are illustrated by the polygons embedding these two sets of species.

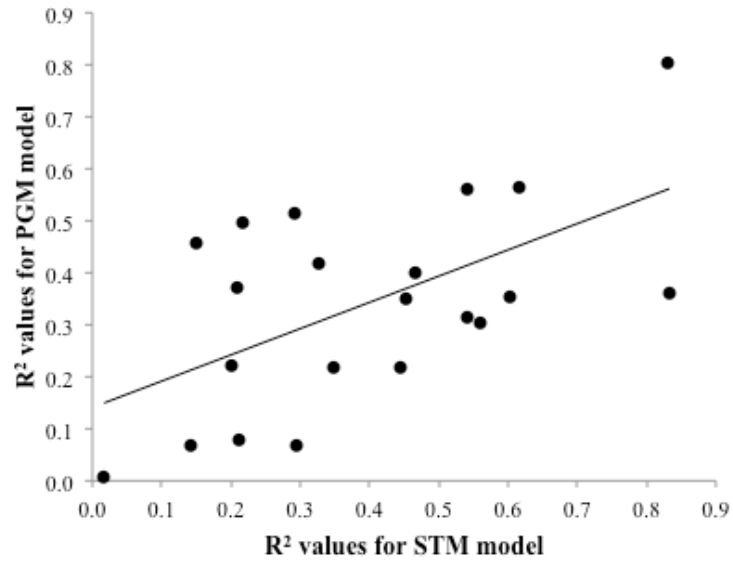


FIG. S5. Correlation between R^2 values from Santarém (STM) and Paragominas (PGM) structural equation models. $R^2 = 0.33$.

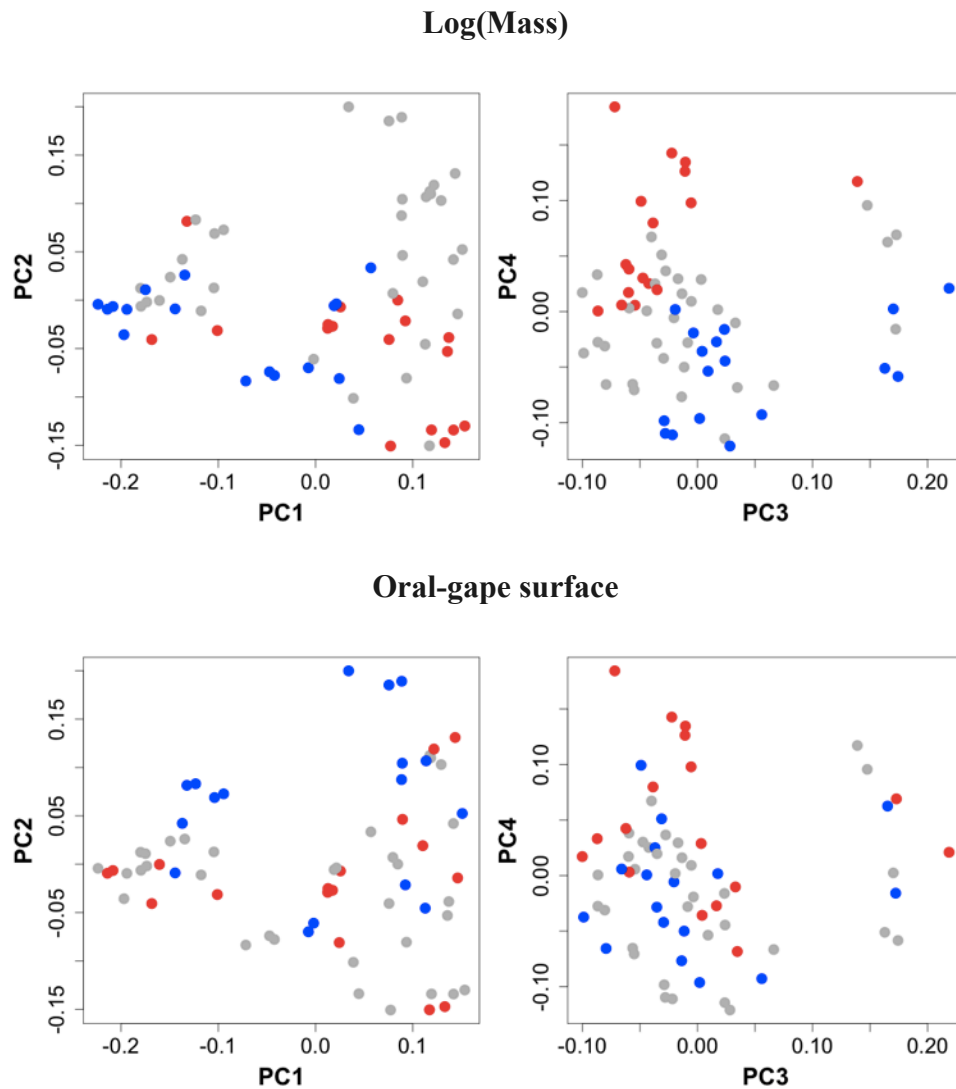


FIG. S6. Four-dimensional representation of the functional space of the regional pool of stream fishes from Santarém (67 species). Each plot represents two axes of a Principal Coordinate Analysis (PC), where species are plotted with dots according to their respective trait values. Species with high (superior quartile) and low (inferior quartile) values for each continuous ecomorphological trait are highlighted in red and blue, respectively. See specific legend to ordinal and nominal traits below respective plots.

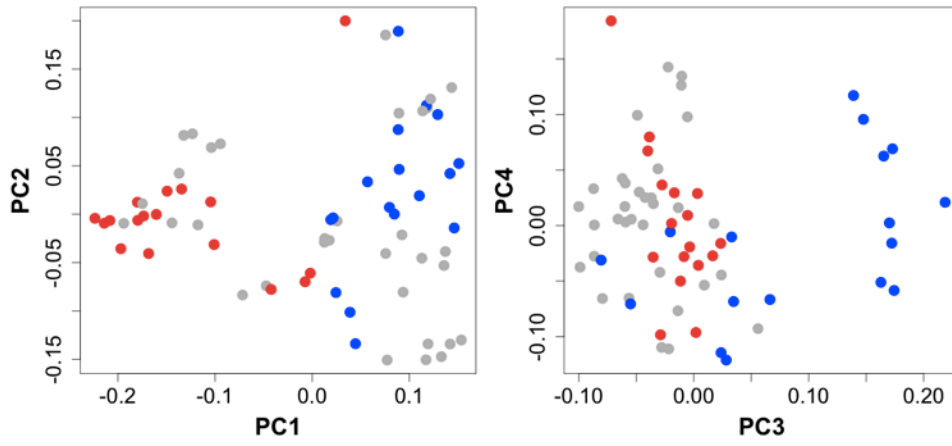
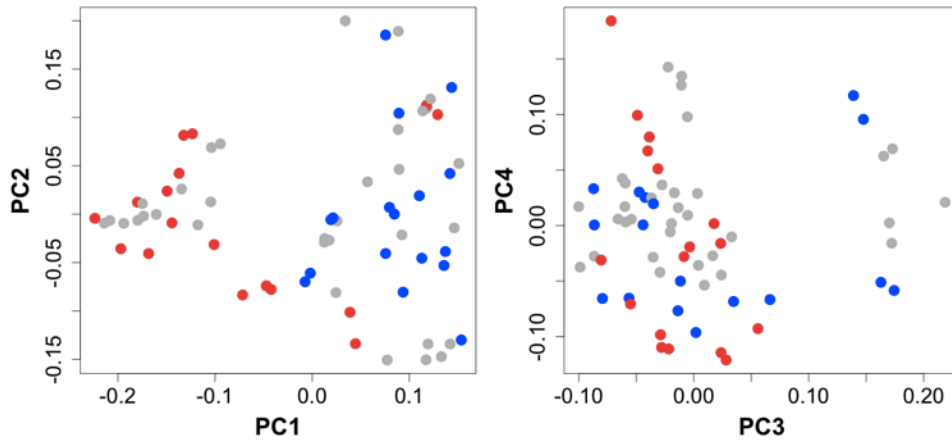
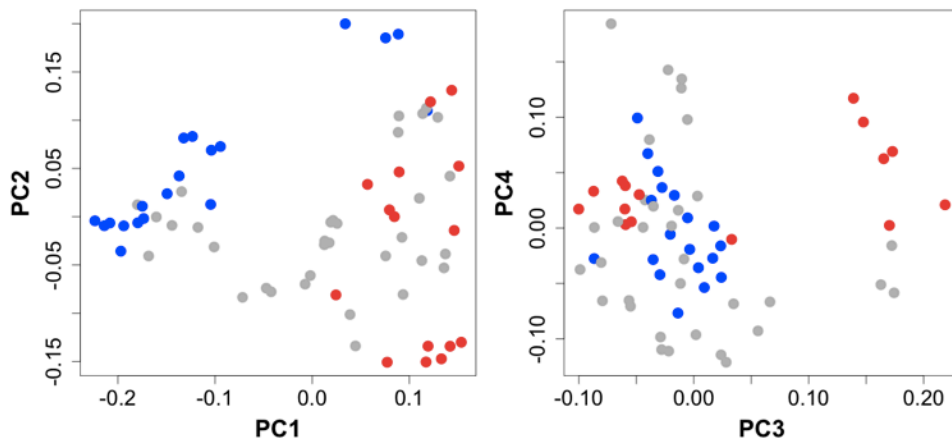
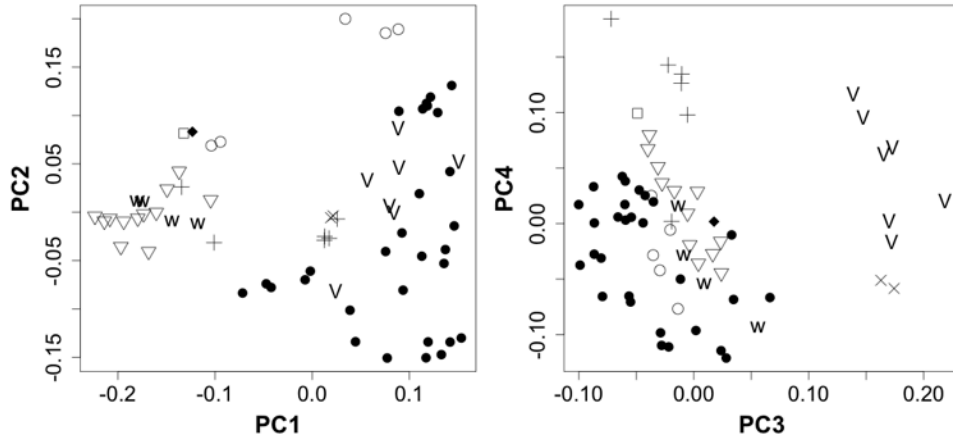
Oral-gape shape**Oral-gape position****Number of teeth**

FIG. S6. (continuation)

Teeth shape



Raker shape

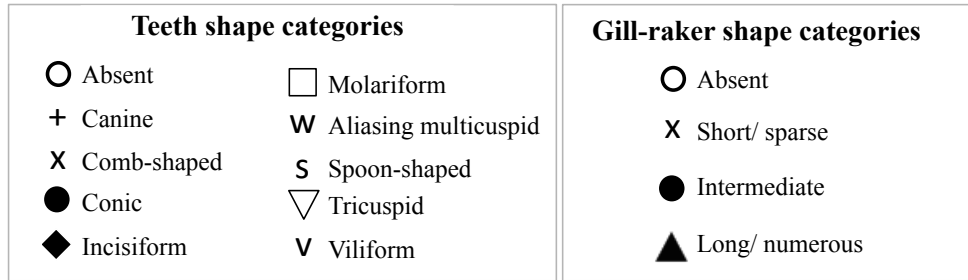
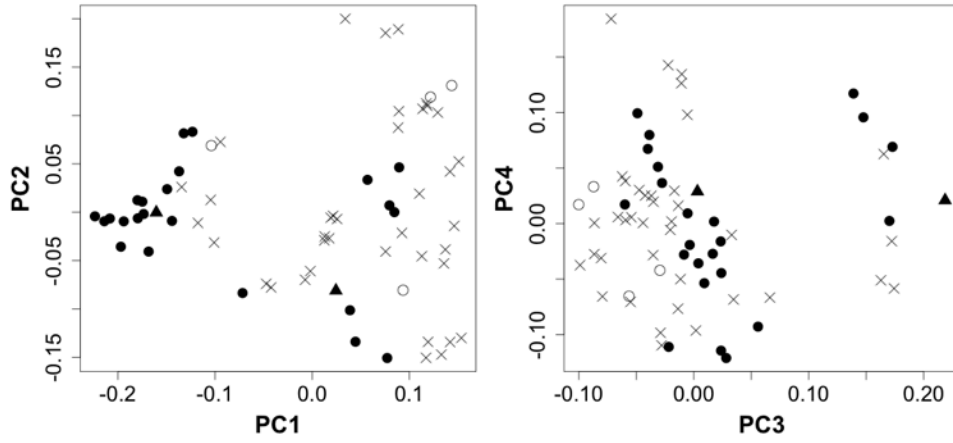
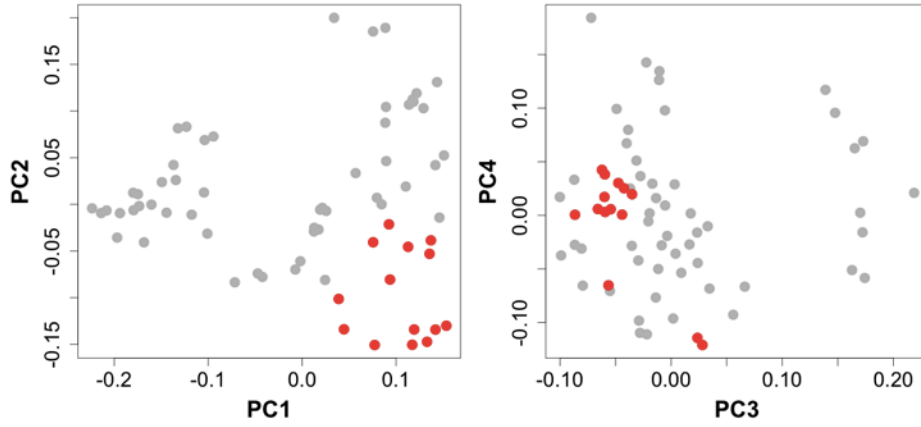
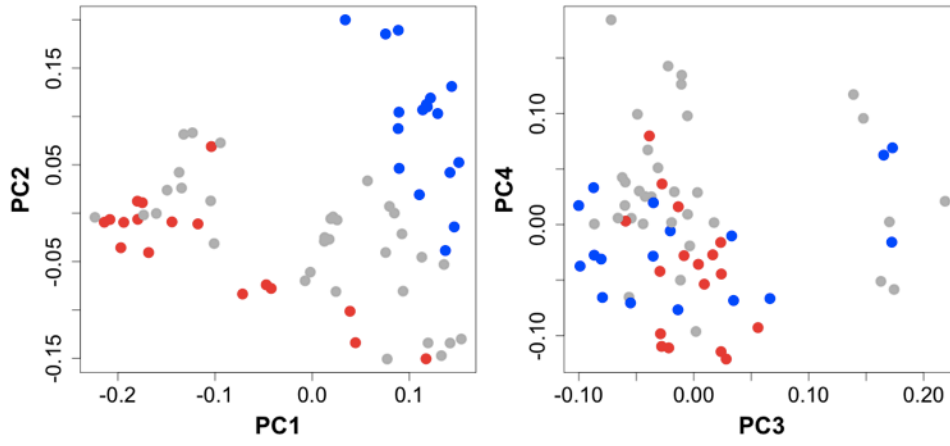


FIG. S6. (continuation)

Protrusion length (trait present only in species marked in red)



Eye size



Eye position

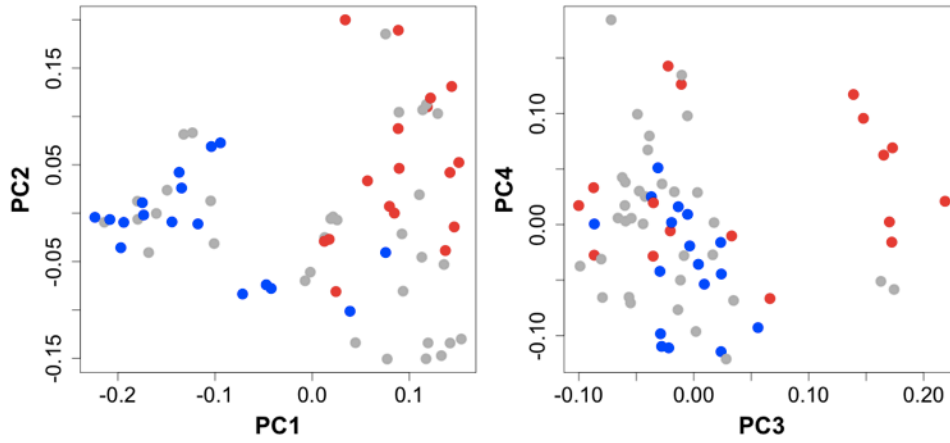
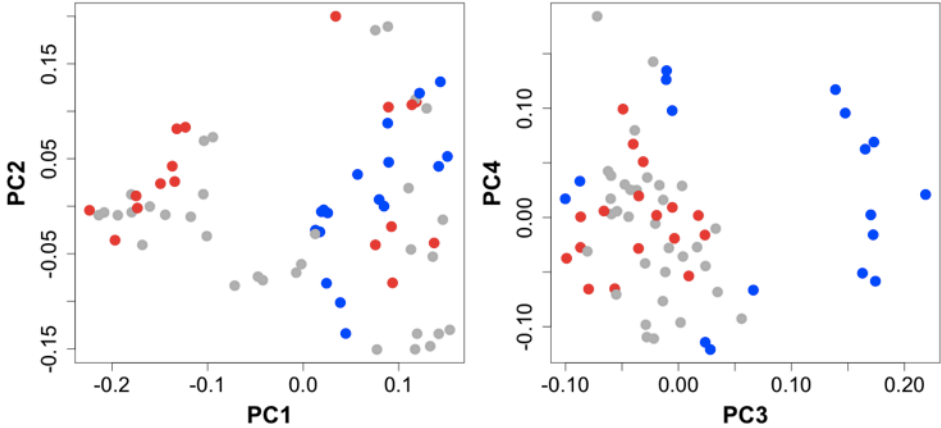
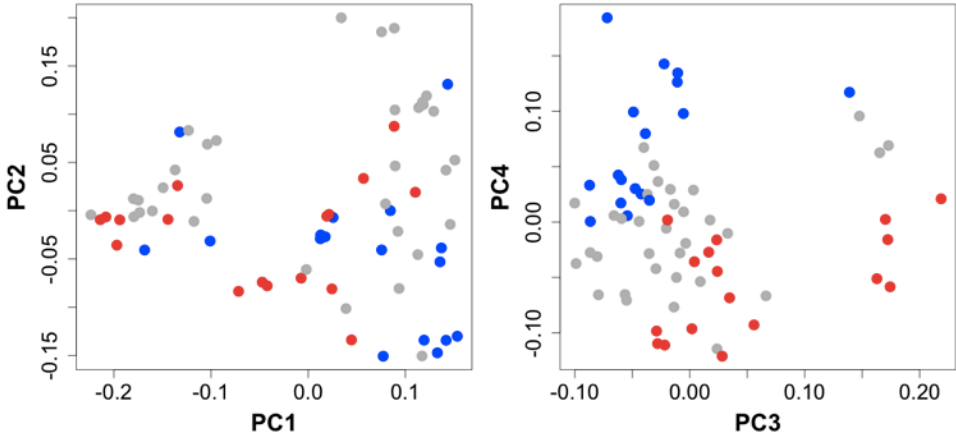


FIG. S6. (continuation)

Body transversal shape



Body transversal surface



Pectoral-fin position

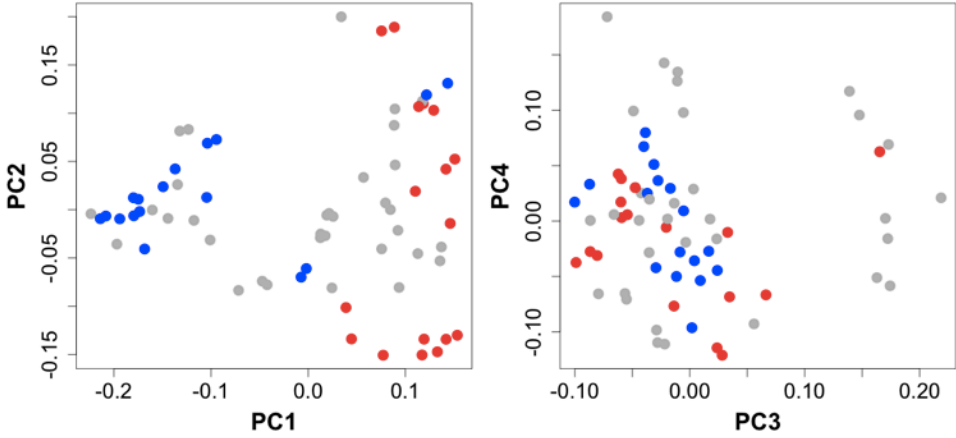
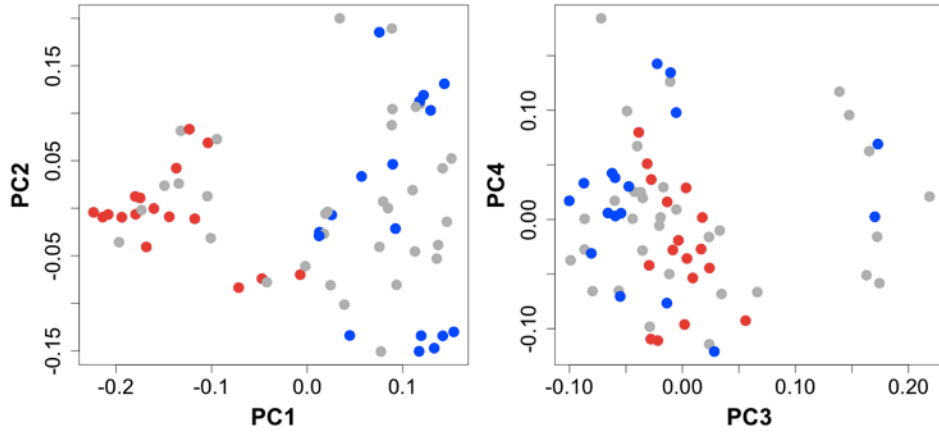
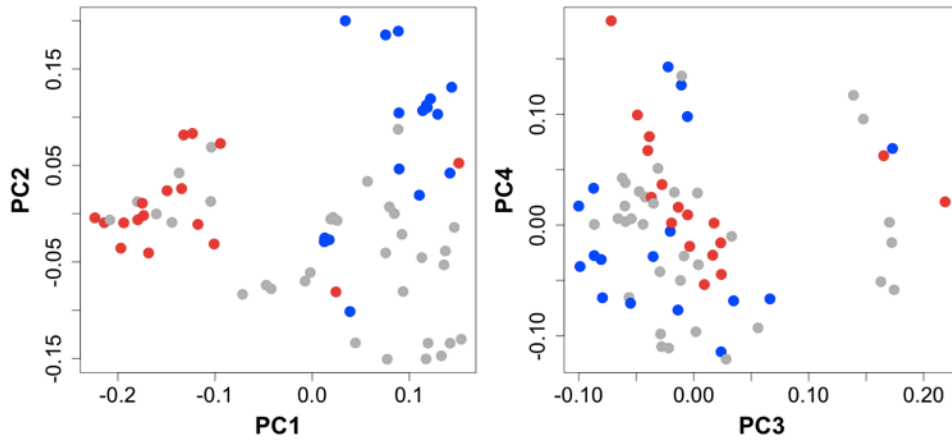


FIG. S6. (continuation)

Aspect ratio of the pectoral fin



Caudal-peduncle throttling



Aspect ratio of the caudal fin

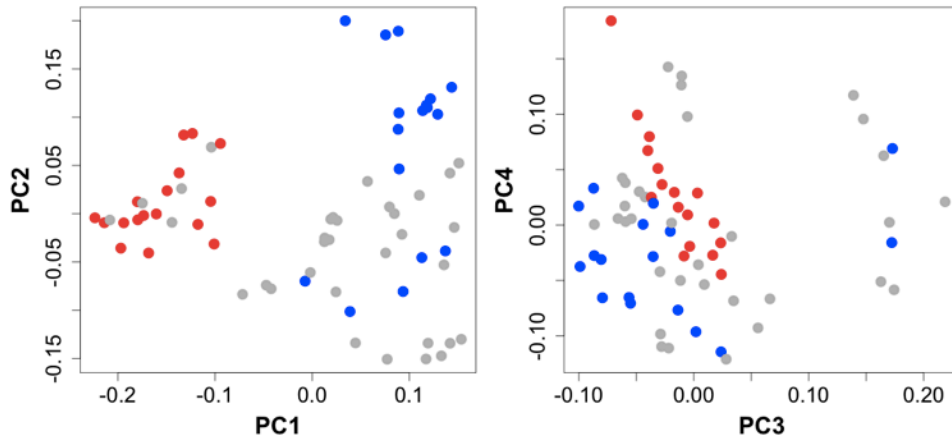
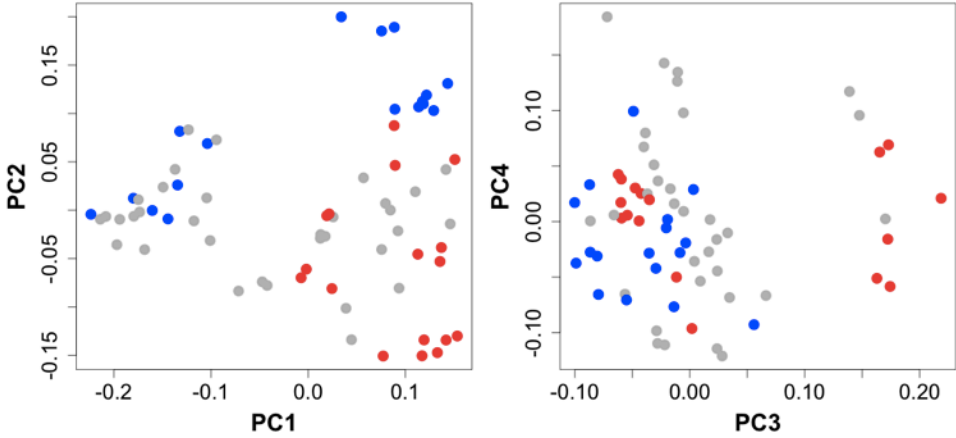


FIG. S6. (continuation)

Fins surface ratio



Fins surface to body size ratio

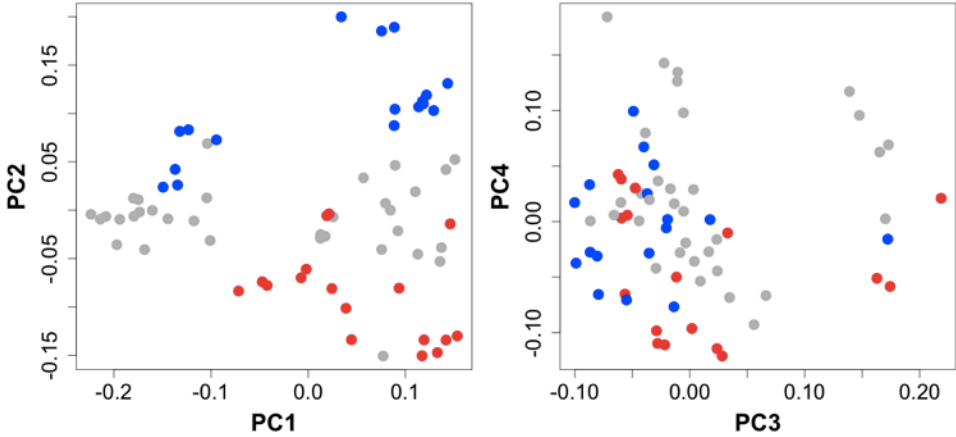


FIG. S6. (continuation)

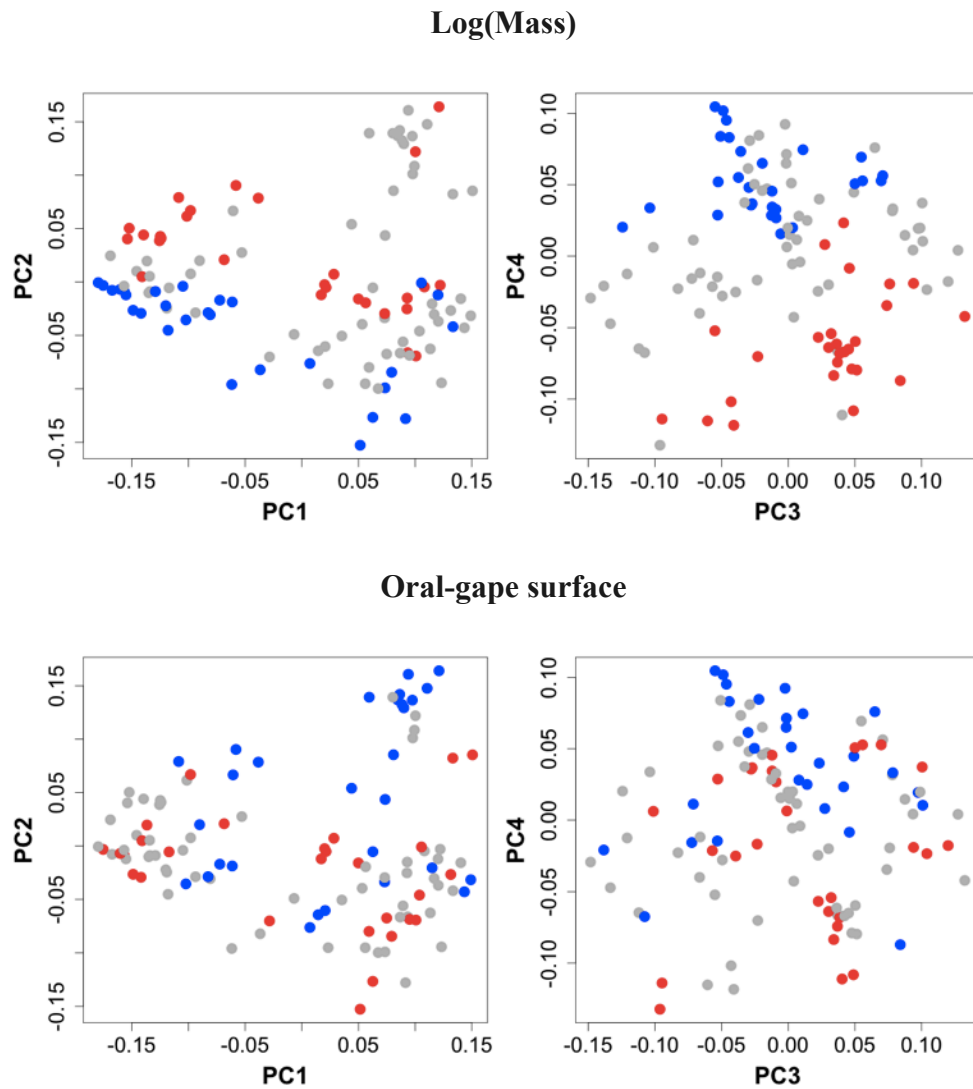


FIG. S7. Four-dimensional representation of the functional space of the regional pool of stream fishes from Paragominas (112 species). Each plot represents two axes of a Principal Coordinate Analysis (PC), where species are plotted with dots according to their respective trait values. Species with high (superior quartile) and low (inferior quartile) values for each continuous ecomorphological trait are highlighted in red and blue, respectively. See specific legend to ordinal and nominal traits below respective plots.

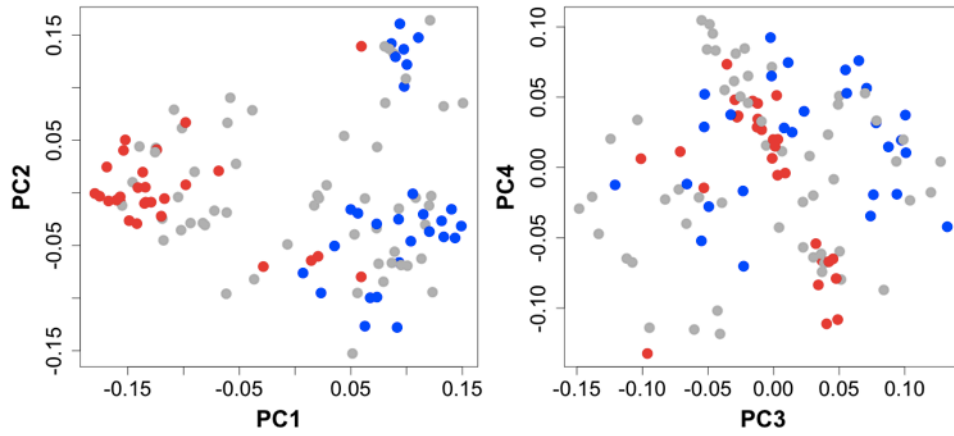
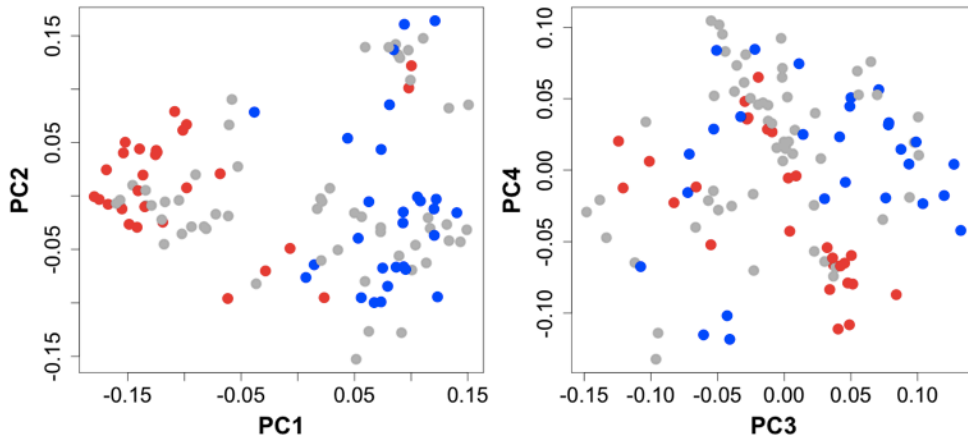
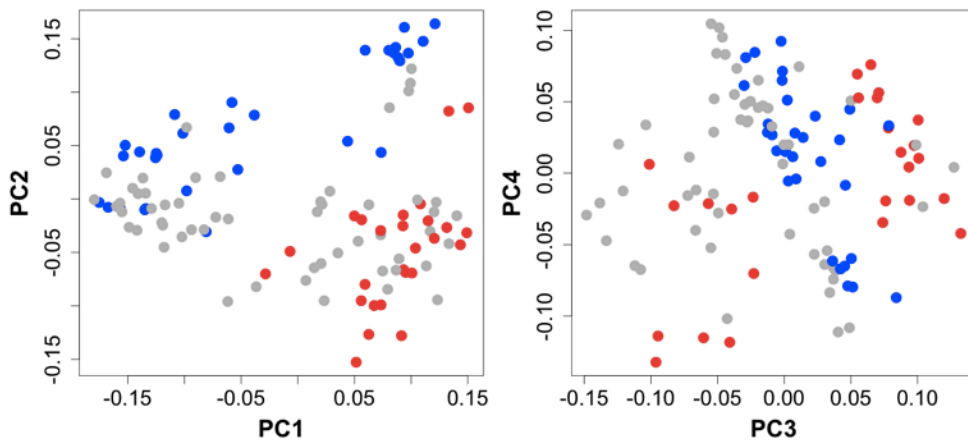
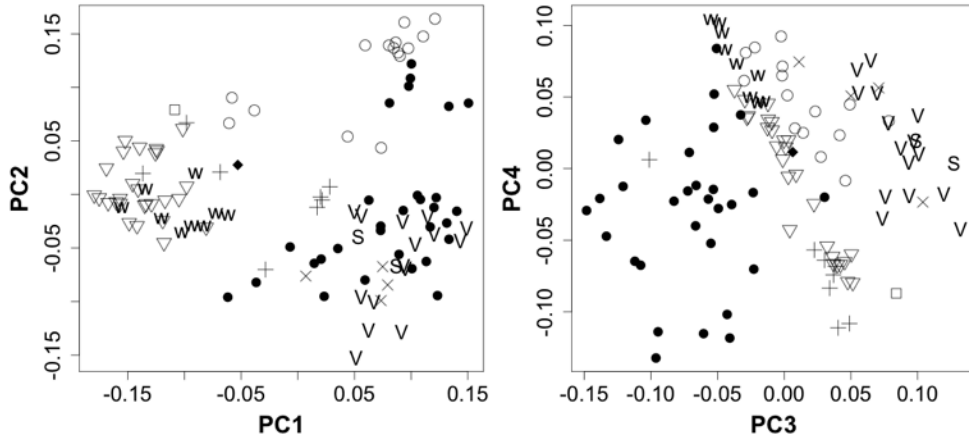
Oral-gape shape**Oral-gape position****Number of teeth**

FIG. S7. (continuation)

Teeth shape



Raker shape

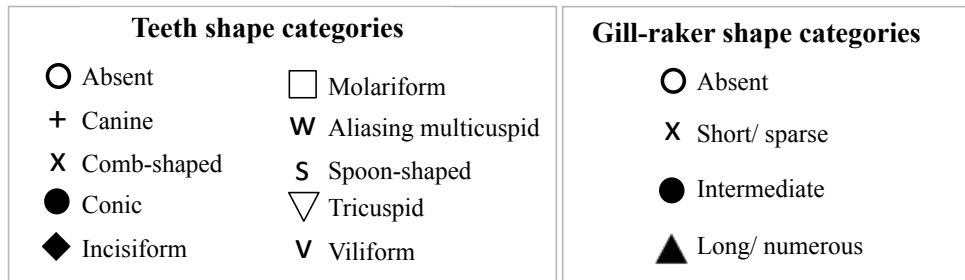
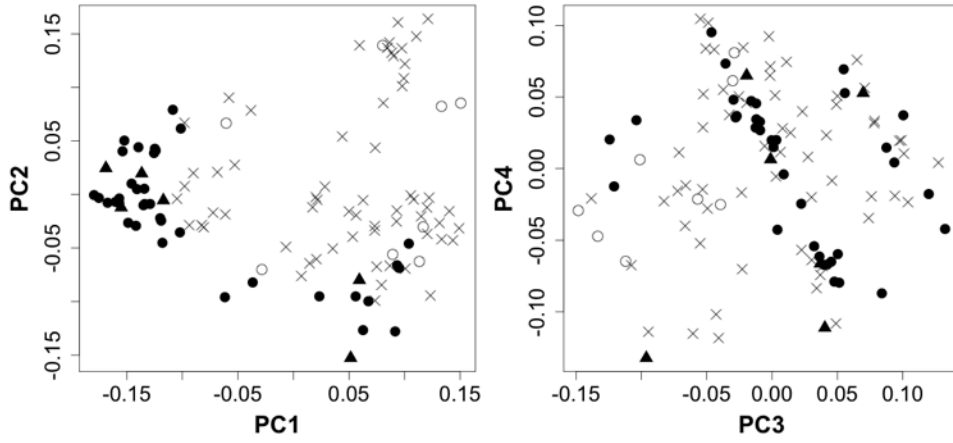
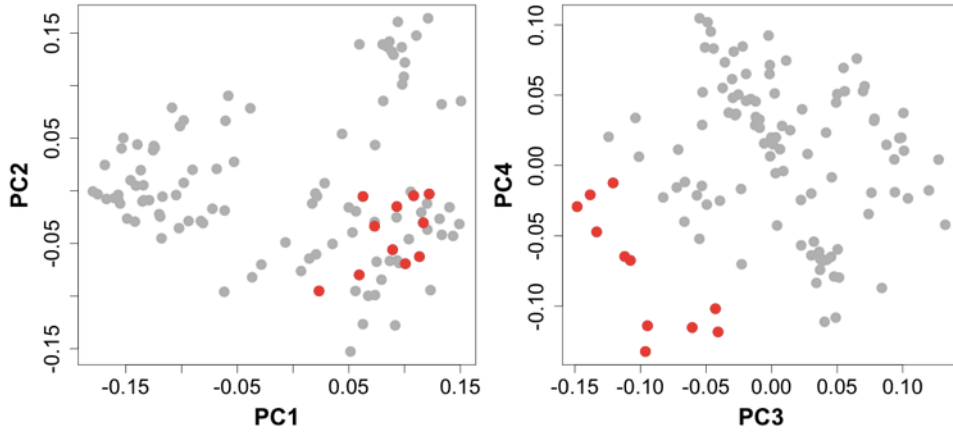
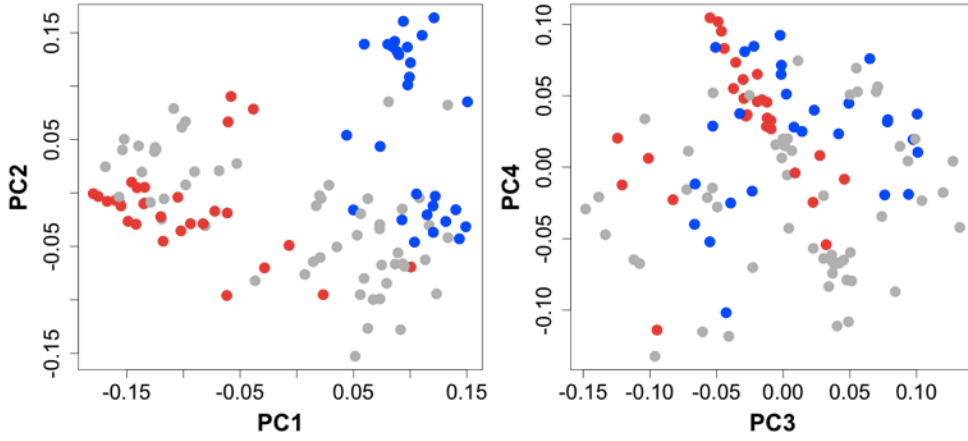


FIG. S7. (continuation)

Protrusion length (trait present only in species marked in red)



Eye size



Eye position

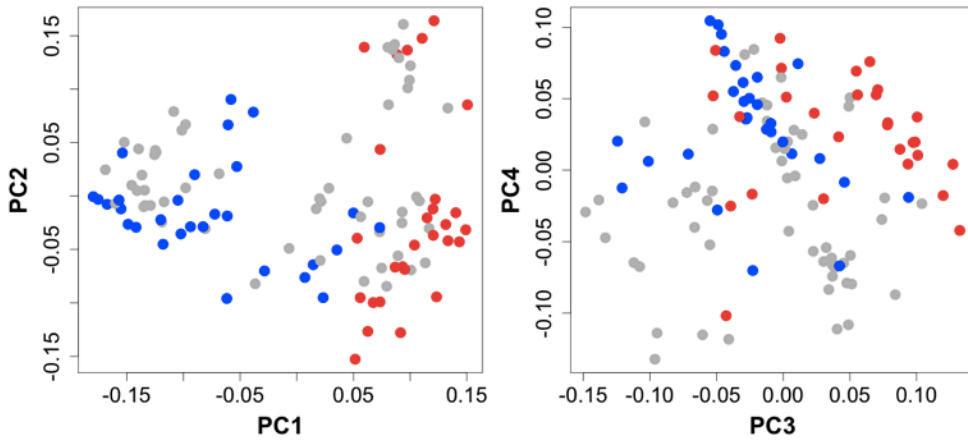
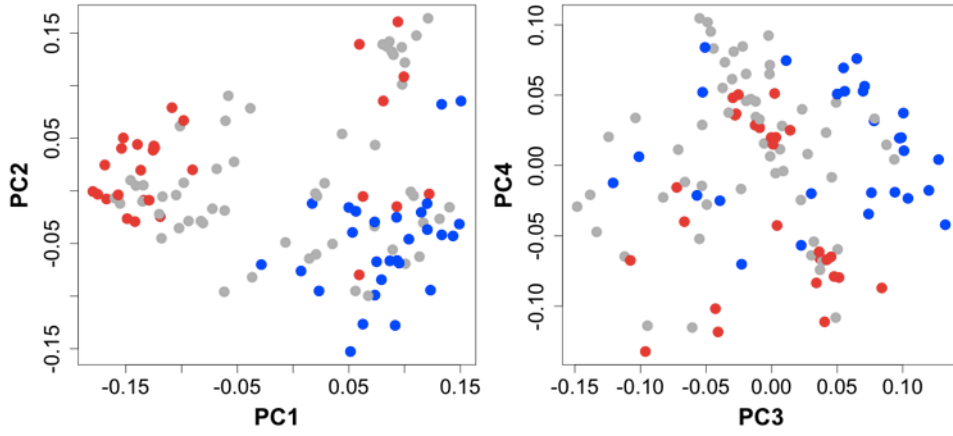
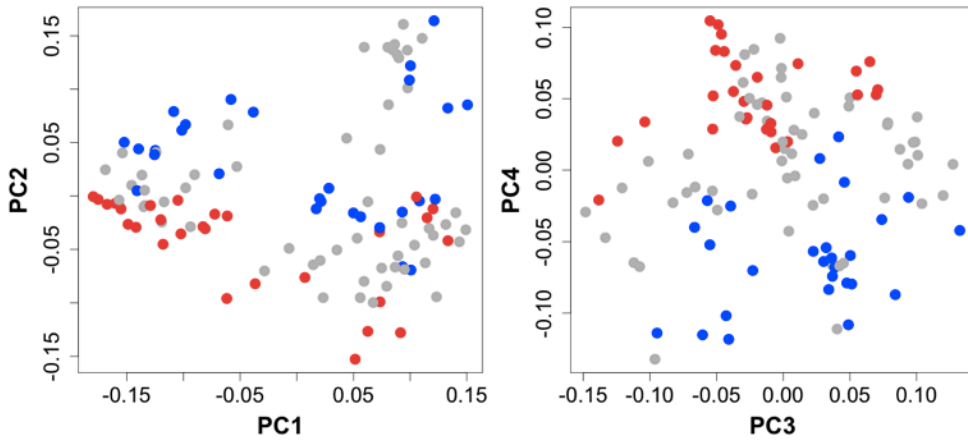


FIG. S7. (continuation)

Body transversal shape



Body transversal surface



Pectoral-fin position

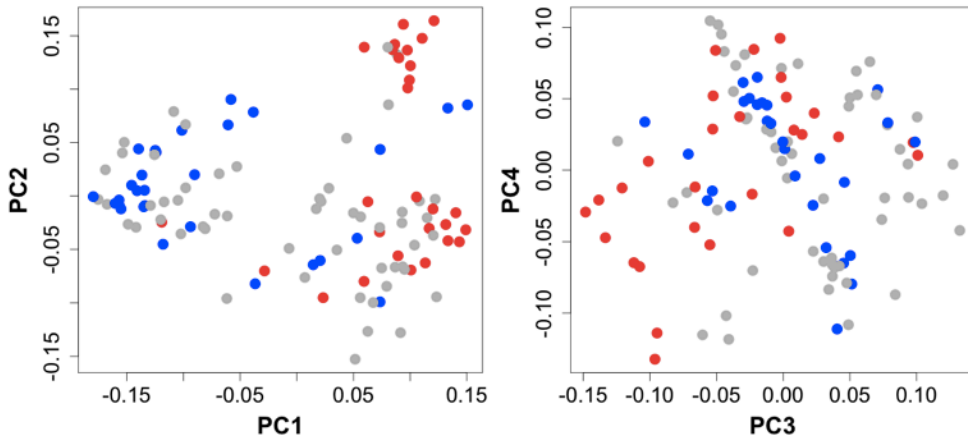
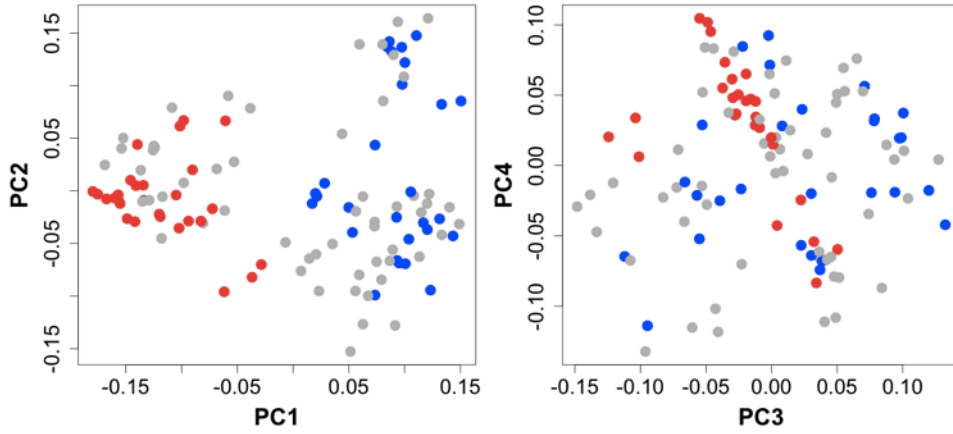
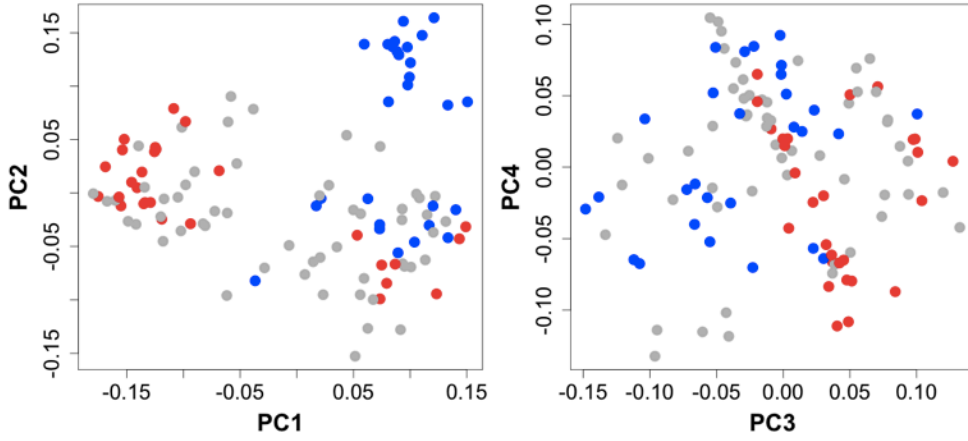


FIG. S7. (continuation)

Aspect ratio of the pectoral fin



Caudal-peduncle throttling



Aspect ratio of the caudal fin

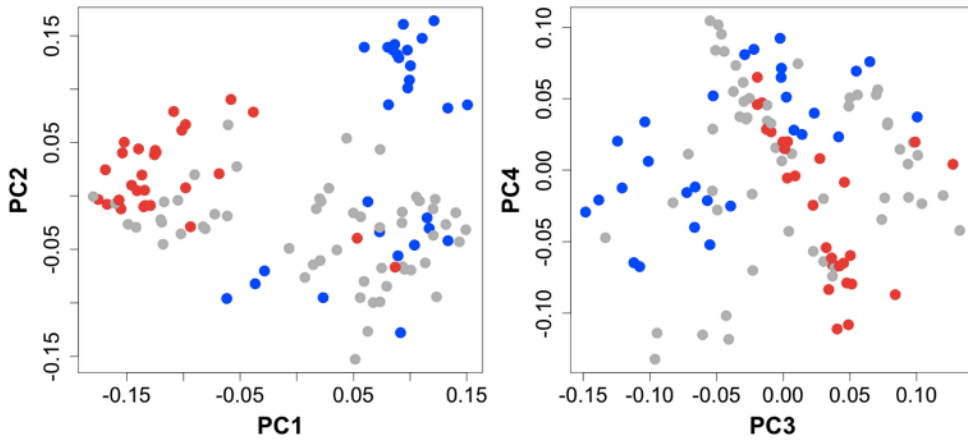
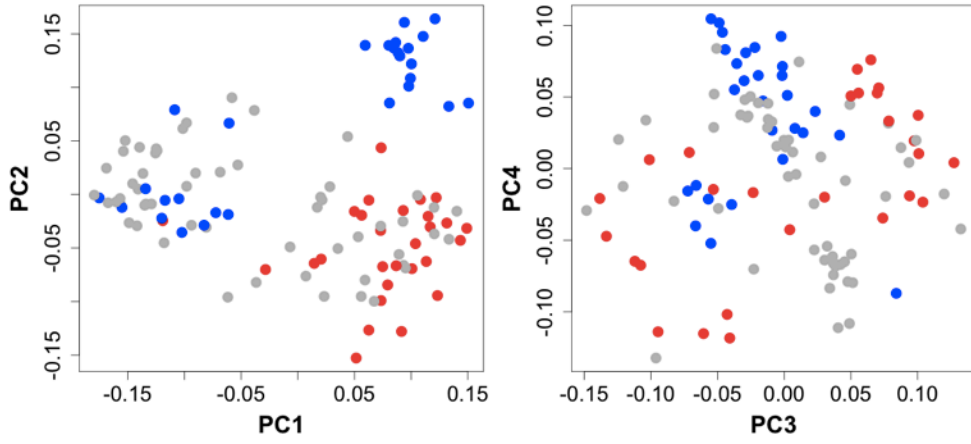


FIG. S7. (continuation)

Fins surface ratio



Fins surface to body size ratio

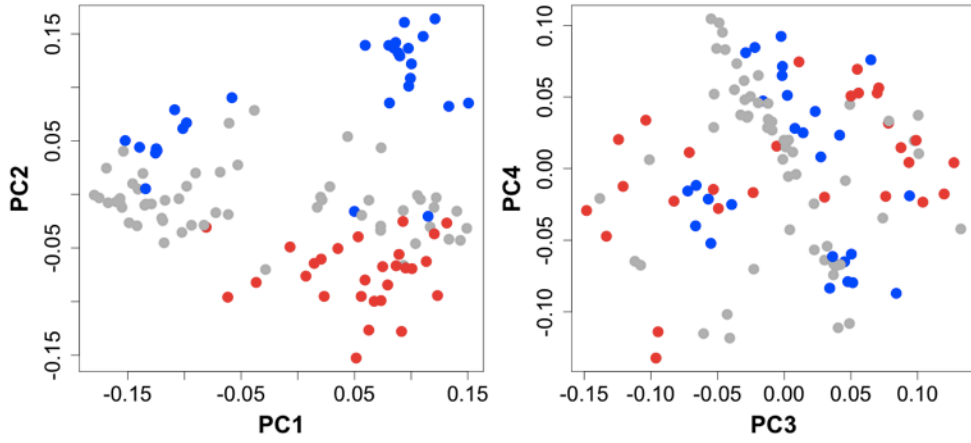


FIG. S7. (continuation)

APPENDIX B

Functional trait assessment

We conducted an ecomorphological analysis to evaluate functional structure in fish assemblages by characterizing species for three key functions: food acquisition, locomotion, and habitat use. Body mass and morphometric measures (Fig. S8) were taken on specimens from 141 species (up to 12 individuals per species), and then combined into 15 ecomorphological traits (Table S1). These traits, except the log-transformed mass, are expressed as unitless ratios, reducing body-size effects. We also assessed the number and shape of teeth and gill rakers on one individual per species. These 18 functional traits are commonly used in functional and ecomorphology studies (Table S1).

We weighed specimens on an electronic balance (0.001 g). Body width, mouth width, mouth depth, snout length and protrusion length were measured with a digital caliper (0.1 mm). The other morphological measures were obtained through the use of digital pictures analyzed in Image J software (0.1 mm). We evaluated gill-raker and teeth characteristics under a binocular microscope.

Although this standard protocol was designed to cover a broad range of morphologies among fish groups (Villéger *et al.* 2010), we had to use some particular conventions. Synbranchiformes and Gymnotiformes (except Apterontidae) have no caudal fin, so the *Aspect ratio of the caudal fin*, *Fins surface ratio*, and *Caudal peduncle throttling* were fixed to 0. Synbranchiformes also have no pectoral fins, so *Pectoral fin position*, *Aspect ratio of the pectoral fin*, and *Fins surface to body size ratio* were fixed to 0.

Voucher specimens are deposited at the INPA Fish Collection, Manaus, and at the UFLA Ichthyological Collection, Lavras, Brazil.

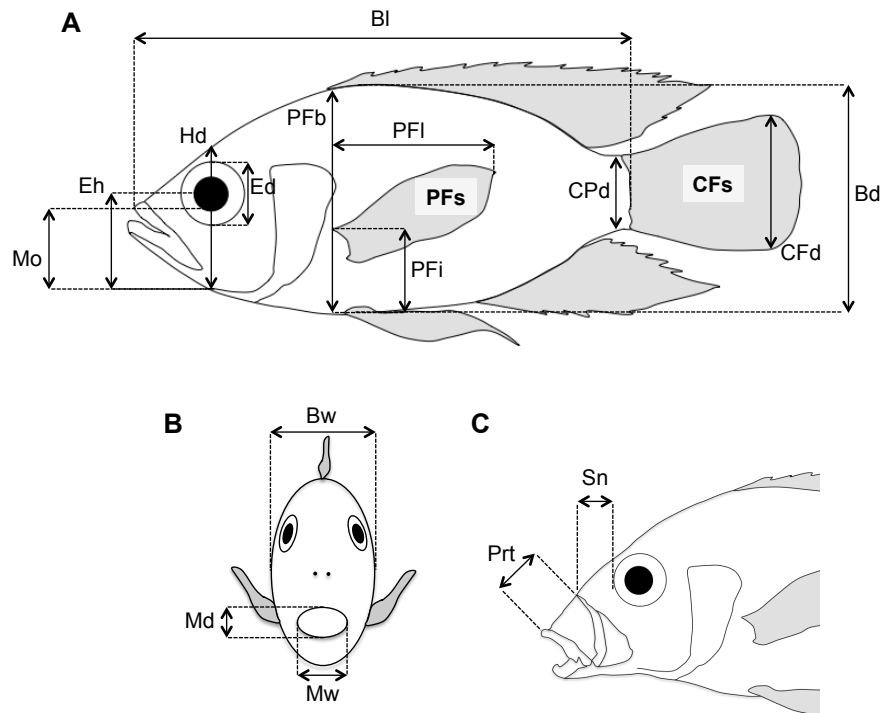


FIG. S8. Morphological traits measured for fish from digital pictures (A): *Bd* body depth, *CPd* caudal-peduncle minimal depth, *CFd* caudal-fin depth, *CFs* caudal-fin surface, *PFi* distance between the insertion of pectoral fin to the bottom of the body, *PFb* body depth at the level of the pectoral-fin insertion, *PFl* pectoral-fin length, *PFs* pectoral-fin surface, *Hd* head depth along the vertical axis of the eye, *Ed* eye diameter, *Eh* distance between the center of the eye to the bottom of the head, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis; and with digital caliper (B, C): *Bw* body width, *Md* mouth depth, *Mw* mouth width, *Sn* snout length, *Prt* protrusion length.

TABLE S1. List of the 18 functional traits measured for stream fishes from the eastern Amazon. Codes for morphological measures are shown in Fig. S8.

Functional trait	Calculation/ Class	Nature	Ecological meaning	References
Teeth shape	Absent	Nominal	Nature of food items captured and feeding method	adapted from Gatz (1979); Keenleyside (1979); Sazima (1986)
	Canine			
	Comb-shaped			
	Conic			
	Incisiform			
	Molariform			
	Multicuspid			
	Spoon-shaped			
	Tricuspid			
Viliform				
Number of teeth	Mean number of teeth between upper and lower jaws	Continuous	Nature of food items captured and feeding method	adapted from Gatz (1979)
Gill-raker shape	Absent Short/ sparse	Ordinal	Filtering ability and gill protection	adapted from Sibbing &

	Intermediate Long/ numerous			Nagelkerke (2001)
Protrusion length	$\frac{Prt}{Sn}$	Continuous	Nature of food items captured and feeding method	adapted from Gatz (1979)
Oral-gape surface	$\frac{Mw \times Md}{Bw \times Bd}$	Continuous	Nature/Size of food items captured	adapted from Karpouzi & Stergiou (2003)
Oral-gape shape	$\frac{Md}{Mw}$	Continuous	Method to capture food items	Karpouzi & Stergiou (2003)
Oral-gape position	$\frac{Mo}{Hd}$	Continuous	Feeding method in the water column	adapted from Sibbing & Nagelkerke (2001)
Eye size	$\frac{Ed}{Hd}$	Continuous	Prey detection	adapted from Boyle & Horn (2006)
Eye position	$\frac{Eh}{Hd}$	Continuous	Vertical position in the water column	Gatz (1979)
Body transversal shape	$\frac{Bd}{Bw}$	Continuous	Vertical position in the water column and hydrodynamism	Sibbing & Nagelkerke (2001)
Body transversal surface	$\frac{\ln [(\frac{\pi}{4} \times Bw \times Bd) + 1]}{\ln (\text{Mass} + 1)}$	Continuous	Mass distribution along the body for hydrodynamism	Villéger <i>et al.</i> (2010)
Pectoral-fin position	$\frac{PFi}{PFb}$	Continuous	Pectoral fin use for maneuverability	Dumay <i>et al.</i> (2004)
Aspect ratio of the pectoral fin	$\frac{PFl^2}{PFs}$	Continuous	Pectoral fin use for propulsion	adapted from Fulton <i>et al.</i> (2001)
Caudal fin- peduncle depth ratio	$\frac{CFd}{CPd}$	Continuous	Caudal propulsion efficiency through reduction of drag	Webb (1984)
Aspect ratio of the caudal fin	$\frac{CFd^2}{CFs}$	Continuous	Caudal fin use for propulsion and/or direction	Webb (1984)
Fins surface ratio	$\frac{2 \times PFs}{CFs}$	Continuous	Main type of propulsion between caudal and pectoral fins	Villéger <i>et al.</i> (2010)
Fins surface to body size ratio	$\frac{(2 \times PFs) + CFs}{\frac{\pi}{4} \times Bw \times Bd}$	Continuous	Acceleration and/or maneuverability efficiency	Villéger <i>et al.</i> (2010)
Mass	$\log (\text{Mass} + 1)$	Continuous	Metabolism, endurance and swimming ability	Villéger <i>et al.</i> (2010)

Supplementary references

- Boyle, K.S. & Horn, M.H. (2006). Comparison of feeding guild structure and ecomorphology of intertidal fish assemblages from central California and central Chile. *Mar. Ecol. Prog. Ser.*, 319, 65–84.
- Dumay, O., Tari, P.S., Tomasini, J.A. & Mouillot, D. (2004). Functional groups of lagoon fish species in Languedoc Roussillon, southern France. *J. Fish Biol.*, 64, 970–983.
- Fulton, C.J., Bellwood, D.R. & Wainwright, P.C. (2001). The relationship between swimming ability and habitat use in wrasses (Labridae). *Mar. Biol.*, 139, 25–33.
- Gatz, A.J. (1979). Community organization in fishes as indicated by morphological features. *Ecology*, 60, 711–718.
- Karpouzi, V.S. & Stergiou, K.I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *J. Fish Biol.*, 62, 1353–1365.
- Keenleyside, M.H.A. (1979). *Diversity and adaptation in fish behaviour*. Springer-Verlag, Berlin, pp. 17–43.
- Sazima, I. (1986). Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *J. Fish Biol.*, 29, 53–65.
- Sibbing, F.A., & Nagelkerke, L.A.J. (2001). Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Rev. Fish Biol. Fisher.*, 10, 393–437.
- Villéger, S., Miranda, J.R., Hernandez, D.F. & Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.*, 20, 1512–1522.
- Webb, P.W. (1984). Form and function in fish swimming. *Sci. Am.*, 251, 72–82.

APPENDIX C

Taxonomic composition and species abundance of fish assemblages from Santarém and Paragominas streams, mid-eastern Amazon.

ORDER	FAMILY	SPECIES	COD.SP	Santarém	Paragominas
Beloniformes	Belontiidae	<i>Potamorhaphis eigenmanni</i>	pot.eige	-	1
Characiformes	Acestrorhynchidae	<i>Acestrorhynchus falcatus</i>	ace.falc	3	28
	Anostomidae	<i>Leporinus friderici</i>	lep.frid	-	36
	Characidae	<i>Astyanax cf. bimaculatus</i>	ast.cf.bima	-	49
		<i>Astyanax maculisquamis</i>	ast.macu	23	-
		<i>Bario steindachneri</i>	bar.stei	-	8
		<i>Bryconops caudomaculatus</i>	bry.caud	284	612
		<i>Bryconops melanurus</i>	bry.mela	211	401
		<i>Charax leticiae</i>	cha.leti	-	46
		<i>Gymnocorymbus thayeri</i>	gym.thay	-	33
		<i>Hemigrammus bellottii</i>	hem.bell	-	526
		<i>Hemigrammus guyanensis</i>	hem.guya	-	539
		<i>Hemigrammus levis</i>	hem.levi	2	255
		<i>Hemigrammus ocellifer</i>	hem.ocel	275	230
		<i>Hemigrammus rhodostomus</i>	hem.rhod	-	68
		<i>Hemigrammus rodwayi</i>	hem.rodw	-	3355
		<i>Hemigrammus sp. "geisleri"</i>	hem.sp.geis	-	595
		<i>Hemigrammus sp. "prata"</i>	hem.sp.prat	-	58
		<i>Hemigrammus stictus</i>	hem.stic	1	-
		<i>Hemigrammus vorderwinkleri</i>	hem.vord	4	-
		<i>Hyphessobrycon copelandi</i>	hyp.cope	-	6
		<i>Hyphessobrycon heterorhabdus</i>	hyp.hete	566	2879
		<i>Hyphessobrycon sp. "tuliio"</i>	hyp.sp.tuli	1222	-
		<i>Iguanodectes rachovii</i>	igu.rach	-	409
		<i>Iguanodectes variatus</i>	igu.vari	240	-
		<i>Jupiaba anteroides</i>	jup.ante	-	26
		<i>Knodus cf. victoriae</i>	kno.cf.vict	-	133
		<i>Knodus savannensis</i>	kno.sava	753	-
		<i>Knodus sp.n. "anal longa"</i>	kno.sp.anlo	-	183
		<i>Microchemobrycon geisleri</i>	mic.geis	-	14
		<i>Moenkhausia celibela</i>	moe.celi	9	-
		<i>Moenkhausia collettii</i>	moe.coll	-	1146
		<i>Moenkhausia collettii "alta"</i>	moe.coll.alta	1160	-
		<i>Moenkhausia comma</i>	moe.comm	23	54
		<i>Moenkhausia oligolepis</i>	moe.olig	-	388
		<i>Moenkhausia sp. "lepidura curta"</i>	moe.sp.lepcu	-	218
		<i>Phenacogaster cf. pectinatus</i>	phe.cf.pect	-	51
		<i>Phenacogaster cf. wayana</i>	phe.cf.waya	-	1
		<i>Poptella brevispina</i>	pop.brev	-	56
		<i>Poptella compressa</i>	pop.comp	-	6
		<i>Pristella maxillaris</i>	pris.maxi	-	69
		<i>Serrapinnus aff. piaba</i>	ser.aff.piab	-	646
	Crenuchidae	<i>Characidium aff. pteroides</i>	cha.aff.pter	18	-
		<i>Characidium cf. etheostoma</i>	cha.cf.ethe	-	257
		<i>Crenuchus spilurus</i>	cre.spil	13	5
		<i>Melanocharacidium dispilomma</i>	mel.disp	9	3
		<i>Microcharacidium weitzmani</i>	mic.weit	-	284
	Curimatidae	<i>Curimatopsis macrolepis</i>	cur.macr	33	45
		<i>Cyphocharax gouldingi</i>	cyp.goul	2	86
		<i>Steindachnerina amazonica</i>	ste.amaz	-	214
	Erythrinidae	<i>Erythrinus erythrinus</i>	ery.eryt	33	34
		<i>Hoplerythrinus unitaeniatus</i>	hop.unit	1	8
		<i>Hoplias curupira</i>	hop.curu	15	1
		<i>Hoplias malabaricus</i>	hop.mala	33	46
	Gasteropelecidae	<i>Gasteropelecus sternicla</i>	gas.ster	-	13
	Lebiasinidae	<i>Copella arnoldi</i>	cop.arno	-	140
		<i>Copella nigrofasciata</i>	cop.nigr	90	-
		<i>Copella sp. "pyrr"</i>	cop.sp.pyrr	11	-
		<i>Nannostomus beckfordi</i>	nan.beck	-	452
		<i>Nannostomus eques</i>	nan.eque	-	11
		<i>Nannostomus marginatus</i>	nan.marg	232	-
		<i>Nannostomus nitidus</i>	nan.niti	-	56
		<i>Nannostomus trifasciatus</i>	nan.trif	-	116
		<i>Pyrrhulina aff. brevis</i>	pyr.aff.brev	-	488
		<i>Pyrrhulina zigzag</i>	pyr.zigz	2	-
	Serrasalminidae	<i>Myloplus rubripinnis</i>	myl.rubr	3	13
		<i>Serrasalmus rhombeus</i>	ser.rhom	-	3
		<i>Serrasalmus sp. "robertsoni"</i>	ser.sp.robe	2	-
		<i>Tometes sp.</i>	tom.sp	3	-

ORDER	FAMILY	SPECIES	COD.SP	Santarem	Paragominas		
Cyprinodontiformes	Rivulidae	<i>Rivulus cf. urophthalmus</i>	riv.cf.urop	27	103		
		<i>Rivulus dibaphus</i>	riv.diba	341	-		
Gymnotiformes	Apteronotidae	<i>Apteronotus albifrons</i>	apt.albi	1	-		
	Gymnotidae	<i>Gymnotus carapo</i>	gym.cara	6	43		
		<i>Gymnotus coropinae</i>	gym.coro	105	74		
	Hypopomidae	<i>Brachyhypopomus beebei</i>	bra.beeb	-	2		
		<i>Brachyhypopomus brevirostris</i>	bra.brev	5	22		
		<i>Brachyhypopomus</i> sp. " <i>regani</i> "	bra.sp.rega	-	40		
		<i>Brachyhypopomus</i> sp. " <i>royeroi</i> "	bra.sp.roye	-	7		
		<i>Brachyhypopomus</i> sp. <i>electropomus</i>	bra.sp.elec	-	1		
		<i>Hypopygus lepturus</i>	hyp.lept	54	77		
		<i>Microsternarchus bilineatus</i>	mic.bili	-	15		
	Rhamphichthyidae	<i>Steatogenys duidae</i>	ste.duid	-	4		
		<i>Gymnorhamphichthys petiti</i>	gym.peti	59	76		
	Sternopygidae	<i>Rhamphichthys marmoratus</i>	rha.marm	-	1		
		<i>Eigenmannia</i> aff. <i>trilineata</i>	eig.aff.tril	8	469		
		<i>Sternopygus macrurus</i>	ste.macr	3	30		
	Perciformes	Cichlidae	<i>Acaronia nassa</i>	aca.nass	1	-	
			<i>Aequidens epae</i>	aeq.epae	84	-	
<i>Aequidens tetramerus</i>			aeq.tetr	113	225		
<i>Apistogramma</i> aff. <i>regani</i>			api.aff.rega	-	143		
<i>Apistogramma agassizii</i>			api.agas	-	17		
<i>Apistogramma caetei</i>			api.caet	-	347		
<i>Apistogramma taeniata</i>			api.taen	239	-		
<i>Cichla kelberi</i>			cic.kelb	-	1		
<i>Crenicichla</i> aff. <i>lepidota</i>			cre.aff.lepi	2	-		
<i>Crenicichla</i> aff. <i>menezesi</i>			cre.aff.mene	73	207		
<i>Crenicichla inpa</i>			cre.inpa	5	-		
<i>Crenicichla johanna</i>			cre.joha	1	-		
<i>Crenicichla strigata</i>			cre.stri	1	-		
<i>Geophagus altifrons</i>			geo.alti	-	11		
<i>Heros notatus</i>			her.nota	-	2		
<i>Hypselecara temporalis</i>			hyp.temp	5	-		
<i>Mesonauta festivus</i>			mes.fest	1	-		
<i>Nannacara taenia</i>			nan.taen	-	20		
<i>Satanoperca jurupari</i>			sat.juru	14	29		
Siluriformes			Aspredinidae	<i>Bunocephalus</i> cf. <i>amaurus</i>	bun.cf.amau	4	3
				<i>Bunocephalus coracoideus</i>	bun.cora	-	3
			Auchenipteridae	<i>Tatia</i> aff. <i>dunni</i>	tat.aff.dunn	-	2
				<i>Tatia intermedia</i>	tat.inte	-	4
	<i>Tetranematachthys wallacei</i>	tet.wall		-	2		
	Callichthyidae	<i>Trachelyopterus galeatus</i>	tra.gale	-	17		
		<i>Callichthys callichthys</i>	cal.call	-	13		
		<i>Corydoras julii</i>	cor.juli	-	26		
	Cetopsidae	<i>Corydoras</i> sp. " <i>C24</i> "	cor.sp.c24	-	8		
		<i>Megalechis picta</i>	meg.pict	-	14		
		<i>Denticetopsis seducta</i>	den.sedu	18	2		
	Doradidae	<i>Helogenes marmoratus</i>	hel.marm	119	129		
		<i>Acanthodoras cataphractus</i>	aca.cata	2	8		
	Heptapteridae	<i>Brachyglanis microphthalmus</i>	bra.micr	4	-		
		<i>Gladioglanis conquistador</i>	gla.conq	-	5		
		<i>Imparfinis</i> sp. " <i>linha continua</i> "	imp.sp.lico	-	19		
		<i>Imparfinis stictionotus</i>	imp.stic	-	64		
		<i>Mastiglanis asopos</i>	mas.asop	11	20		
		<i>Pimelodella</i> sp. " <i>sem serra</i> "	pim.sp.sese	-	31		
		<i>Pimelodella</i> sp. " <i>serra forte</i> "	pim.sp.sefo	-	264		
		<i>Rhamdia muelleri</i>	rha.muel	3	14		
		<i>Rhamdia quelen</i>	rha.quel	2	21		
		Loricariidae	<i>Ancistrus</i> sp. " <i>bola</i> "	anc.sp.bl	-	36	
<i>Farlowella platorynchus</i>			far.plat	-	4		
<i>Farlowella schreitmulleri</i>	far.schr		-	34			
<i>Hemiodontichthys acipenserinus</i>	hem.acip		-	1			
<i>Hypostomus</i> cf. <i>cochliodon</i>	hyp.cf.coch		-	1			
<i>Otocinclus hoppei</i>	oto.hopp		-	3			
<i>Parotocinclus</i> sp.	par.sp		2	-			
<i>Parotocinclus</i> sp. " <i>bicudinho</i> "	par.sp.bic		19	-			
<i>Rineloricaria</i> sp. 2 " <i>madeira</i> "	rin.sp2.mad		-	202			
Pseudopimelodidae	<i>Batrochoglanis raninus</i>		bat.rani	1	9		
Trichomycteridae	<i>Ituglanis amazonicus</i>	itu.amaz	3	148			
	<i>Trichomycterus hasemani</i>	tri.hase	-	2			
Synbranchiformes	Synbranchidae	<i>Synbranchus madeirae</i>	syn.made	19	22		
		<i>Synbranchus</i> sp. " <i>pintado</i> "	syn.sp.pint	3	1		

CHAPTER 2

Leitão, R.P.; Zuanon, J.; Villéger, S.; Williams, S.; Baraloto, C.; Fortunel, C.; Mendonça, F.P. & Mouillot, D. Rare species over-contribute to the functional structure of species assemblages. Manuscript submitted to *Diversity and Distributions*.

Rare species over-contribute to the functional structure of species assemblages

Rafael P. Leitão ^{1,2}, Jansen Zuanon ³, Sébastien Villéger ², Stephen Williams ⁴, Christopher Baraloto ⁵, Claire Fortunel ⁶, Fernando P. Mendonça ⁷ and David Mouillot ^{2,8}

Affiliations:

¹ Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, 69060–001 Manaus, Brazil.

² Laboratoire Biodiversité Marine et ses usages, UMR 9190 MARBEC CNRS–UM-IRD–IFREMER, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier, France.

³ Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, 69060–001 Manaus, Brazil.

⁴ Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia.

⁵ INRA, UMR Ecologie des Forêts de Guyane, BP 709, 97387 Kourou Cedex, French Guiana.

⁶ Department of Biology, University of Maryland, College Park, MD, USA.

⁷ Universidade Federal do Amazonas, Instituto de Saúde e Biotecnologia, 69460000 Coari, Brazil.

⁸ Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811 Australia.

E-mail: RPL: ecorafa@gmail.com; JZ: zuanon@inpa.gov.br; SV: sebastien.villeger@univ-montp2.fr; SW: stephen.williams@jcu.edu.au; CB: chris.baraloto@ecofog.gf; CF: fortunel@umd.edu; FPM: fernandopmendonca@gmail.com; DM: david.mouillot@univ-montp2.fr

Running title: Contribution of rare species to biodiversity

Corresponding author: Rafael P. Leitão

Manuscript type: Biodiversity Research

ABSTRACT

Aim There is a global consensus that the diversity of functional traits within species assemblages drives ecosystems functioning, and that rare species are the first to go extinct under ever-increasing human-induced disturbances. Thus, the ecological impacts of functional diversity loss are intimately related to the contribution of rare species to the diversity and distribution of traits within assemblages. Surprisingly, the functional importance of rare species is still poorly known, particularly in tropical species-rich assemblages where a large proportion of species are rare and high rates of species extirpations are expected. In this study, we assessed the contribution of rare species to the functional structure of assemblages, both at the local and the regional scales.

Location Brazilian Amazon, French Guiana, Australian Wet Tropics.

Methods We used three extensive datasets of phylogenetically distinct groups (stream fish, rainforest trees, and birds), and built an integrative measure of rarity vs. commonness for each species, combining local abundance, geographic range, and habitat breadth. Considering species traits and their distributions within a functional space, we assessed three complementary facets of the assemblage functional structure: functional richness, specialization and originality. Using realistic scenarios of species loss and null models we tested whether rare species over- or under-contribute to these functional facets.

Results Rare species tend to have the most extreme and unique combinations of trait values for the three taxonomic groups. We detected disproportionate impacts of rare species extinction on the functional structure of assemblages, both locally and regionally. Losing rare species significantly reduced the functional richness, specialization and originality of assemblages.

Main conclusions Losing rare species may dramatically imperil the rates of ecological processes. The functional over-contribution of rare species justifies the application of the precautionary principle for tropical biodiversity conservation despite the apparent insurance provided by such species-rich systems.

Keywords: Amazon, biodiversity, extinction, functional diversity, functional originality, rarity, specialization, tropics.

INTRODUCTION

All ecosystems on Earth are facing unprecedented levels of disturbance (Vitousek *et al.* 1997) inducing the sixth extinction crisis (Barnosky *et al.* 2011), with rare species often being the most vulnerable (Magurran 2009). Species can be considered rare when they have small population sizes, restricted geographic ranges, or narrow habitat tolerances; these combined characteristics define several forms of rarity (Rabinowitz 1981) and different levels of extinction risk (Harnik *et al.* 2012). Therefore, compared to abundant and widespread species, rare species have greater sensitivity to both natural and human-induced disturbances such as overexploitation, habitat loss and global environmental changes (Purvis *et al.* 2000; Davies *et al.* 2004; Lavergne *et al.* 2005; Sekercioglu *et al.* 2008; Hubbell 2013). Rare species have thus received significant attention from conservation biologists; nevertheless, the functional consequences of their decline remain largely overlooked (Lyons *et al.* 2005).

Beyond the loss of species, there is a growing awareness that the loss of ecological processes that sustain ecosystem functioning can be the most critical impact under accelerating global changes (Naeem *et al.* 2012). The diversity of ecological processes is currently seen as being more closely related to the diversity of functional traits within communities than to the diversity of taxa *per se* since species with different traits are more likely to perform complementary roles (Díaz & Cabido 2001; Hooper *et al.* 2005; Mouillot *et al.* 2011). In this context, considering the high vulnerability of rare species to extinction, a critical issue is to assess their contribution to the diversity and distribution of functional traits within an assemblage, which we refer to the functional structure of assemblages (FS). If rare species mainly support roles that are also played by common species we would expect a low impact following their extinction, whereas their over-contribution to FS may lead to a dramatic loss of ecological processes in case of their extinction.

A recent study showed that in three regional species pools (coral reef fishes, tropical trees, and alpine plants) the most distinct combinations of traits are mainly supported by rare species (Mouillot *et al.* 2013a), which may suggest that they are functionally irreplaceable. At the same time, many rare species were shown to support the most common functions and only add functional redundancy to the system (Mouillot *et al.* 2013a). However, rather than scale up at the assemblage level, Mouillot *et al.* (2013a) focused on an individual species-based metric (functional distinctiveness). There is still no study assessing the consequences of rare

species loss on the multiple facets of assemblage functional structure, investigating different spatial scales and embracing different forms of rarity (but see Jain *et al.* 2014).

Here we built an integrative measure of species rarity vs. commonness (i.e. combining local abundance, geographic range, and habitat breadth) and we considered species traits and their distributions within a functional space (*sensu* Mouillot *et al.* 2013b) to quantitatively assess the contribution of rare species to three complementary facets of assemblage functional structure (Fig. 1): functional richness (Villéger *et al.* 2008), i.e. the extent of trait combinations, which can be viewed as the range of niches filled by the assemblage; functional specialization (Bellwood *et al.* 2006), i.e. the degree of functional distinctiveness of the species in the assemblage; and functional originality (Mouillot *et al.* 2013b), i.e. the mean functional distance of each species to its nearest neighbor, which can be viewed as the opposite of the degree of functional redundancy within the assemblage.

We designed realistic scenarios of species loss, both at the local and regional scales to test whether rare species over- or under-contribute to the FS of species assemblages. If rare species tend to support the most extreme and unique combinations of traits, we expect that their extinction would deeply affect the three functional facets (Fig. 1). Testing these two alternative hypotheses is particularly critical in tropical ecosystems, where a large proportion of species are rare (Hubbell 2013) and high rates of species extirpations are expected in a near future (Brook *et al.* 2006; Fey *et al.* 2015). Therefore, we applied this framework to three extensive datasets of species-rich tropical assemblages to enhance the generality of our findings: stream fishes from the Brazilian Amazon, rainforest trees from French Guiana, and birds from the Australian Wet Tropics.

METHODS

Datasets

The datasets were selected because sampling (1) was carried out in sites covering broad geographic and environmental gradients within well-preserved regions, (2) was standardized for species local abundances and local habitat characterization, (3) included a functional characterization of the species.

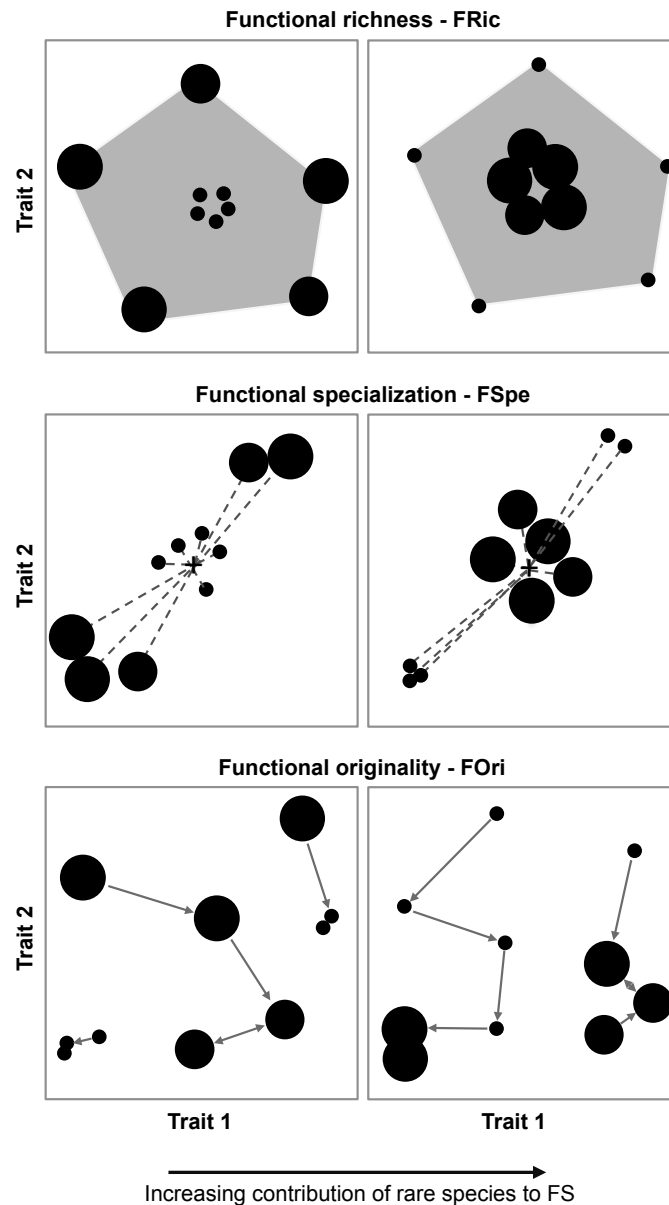


Figure 1 Hypothetical scenarios for the contribution of rare species to the functional structure (FS) of species assemblages. Each plot represents a two-dimensional functional space where dots represent 10 species placed according to their respective trait values. The level of species commonness (accounting for abundance, geographic range and habitat breadth) is illustrated by the size of the dots, rare species being represented by small dots. Three FS indices are illustrated (separately for graphical simplicity): functional richness (the extent of trait combinations, expressed as the convex-hull volume of the functional space filled by all species within the assemblage; gray polygon projected); functional specialization (the degree of distinctiveness of the functional traits in the assemblage, expressed as the mean distance between each species and the average position (black cross) of all species in the functional space; dashed lines indicate individual-species distances); and functional originality (the degree of uniqueness of species traits in the assemblage, expressed as the mean distance between a given species and its nearest neighbor in the functional space; gray arrows indicate individual-species distances). The contribution of rare species to FS increases from the left to the right of the figure in the sense that their loss would significantly reduce the value for each facet.

Fishes

Fishes were sampled in 320 rainforest streams of the Brazilian Amazon between 2004 and 2012, encompassing over 2.3 million km² along the main tributaries of the cis-Andean Amazon basin (long: 46°52'W – 68°25'W; lat: 03°23'N – 11°39'S; see Fig. S1 in Supporting Information). In each stream, we determined a set of 15 environmental parameters describing stream-channel structure, substrate and water quality (see Appendix S1). All streams have small dimensions (2.3 m width and 0.2 m depth on average) allowing for effective sampling of fish abundances within well-delimited habitat boundaries. The stream extremities (50-m long section) were blocked with fine-mesh nets (5 mm) and fishes were caught using seine and hand nets during daylight hours. A total of 395 taxa were counted and identified at the species level. Each species was functionally described using a set of 18 ecomorphological traits related to food acquisition, locomotion, and habitat preferences (adapted from Villéger *et al.* 2010; see Appendix S2).

Trees

Trees were inventoried in 36 lowland rainforest plots (2 ha) in French Guiana between 2009 and 2010. The plots covered common lowland forest habitats of tropical South America (seasonally flooded, non-flooded 'terra firme' and white-sand forests; Baraloto *et al.* 2011) across an area of 15,427 km² (long: 52°13'W – 54°03'W; lat: 04°04'N – 05°29'N; see Fig. S1). The sampling followed modified-Gentry methods as described in Baraloto *et al.* (2013). In each of the 36 plots, we determined a set of 14 environmental parameters describing climate and soil characteristics (see Appendix S1). We then counted and identified all trees ≥ 2.5 cm diameter (at 1.3 m height) in ten 2 m x 50 m belt transects. Given the operational difficulties to thoroughly measure traits in species-rich tree assemblages, we selected six out of the 36 plots that represent the broader environmental gradient within the region to functionally characterize all species (totaling 262 species). This characterization included 15 functional traits describing leaf and wood economics (Fortunel *et al.* 2012; see Appendix S2). Although the functional assessment at local assemblage scale was restricted to those six plots, the estimates of species distribution and abundance (see rarity assessment section below) included all the 36 plots.

Birds

Birds were sampled between 1992 and 2009 in the Australian Wet Tropics (AWT), a bioregion that covers 18,000 km² of mixed tropical forests ranging from sea level to *c.* 1,600 m and running parallel to the North Queensland coast, Australia (long: 144°50'E – 147°10'E; lat: 15°30'S – 19°15'S; see Fig. S1). The region is dominated by rainforests with most of the area protected in the AWT World Heritage Area (Williams *et al.* 2009). Birds were recorded within 1,323 standardized dawn surveys across 180 permanent 150-m transects. Each survey was 30 minutes duration with all individuals counted and identified using calls and visual observations, totaling 86 species. The transects were distributed across 47 sub-regions delimited by Williams *et al.* (2010) to cover elevational, climatic and latitudinal gradients across all the AWT (*c.* 95% of available environmental space in the bioregion). Given that most birds are highly mobile organisms and local-assemblage boundaries are difficult to delimit, we considered each of these 47 sub-regions as local assemblages in this study. Seven traits describing the key aspects of bird's life history and behavior were used to functionally describe the 86 species (traits compiled in Williams *et al.* 2010; see Appendix S2).

Rarity assessment

Different approaches to define species rarity have been proposed, being most frequently based on three primary characteristics: population size or local abundance, geographic range, and habitat specificity or breadth (Rabinowitz 1981). Because they all determine extinction risk while being complementary to each other (Williams *et al.* 2009; Harnik *et al.* 2012) we embedded these three characteristics within an integrated framework to assess rarity vs. commonness species values.

For the three datasets, the local abundance (LA) of each species was determined as the mean number of individuals counted where that species was present (*i.e.* excluding zero values).

For fishes and trees, the geographic range (GR) was estimated by the area (km²) that lies within the outermost geographic limits of the occurrence of each species (*i.e.* 'extend of occurrence' in Gaston 1991), based exclusively on their distribution across our sample sites (*i.e.* 320 streams, 36 plots). For species recorded only in one sample site, GR was defined as the area (km²) of the site in which that species occurs. For species recorded only in two sites, GR was estimated as the extension (km) of the sites multiplied by the geographic distance between them (km). We chose to restrict GR estimates to our own data because secondary

information (e.g. collection and herbarium) lacks for part of both fish and tree species; a lacuna widely recognized for the Amazon forest (Hubbell 2013). For AWT birds, however, species geographic ranges had been previously well established during decades of intensive and oriented studies across the region. Therefore, we used the GR data compiled in Williams *et al.* (2010).

For fishes and trees, the habitat breadth (HB) was estimated by the ‘tolerance’ metric from Outlying Mean Index (OMI) analyses (Dolédec *et al.* 2000), which is a measure of the species-specific niche breadth relative to the available niche space of the study region (i.e. environmental parameters measured across sites). Highly correlated (r -Pearson > 0.5) environmental variables were excluded and site-environmental matrices were scaled and centered before running OMI analysis. For birds, the HB was estimated by the proportion of occurrences in different structural vegetation types for each species (i.e. ‘vegetation specialization’ in Williams *et al.* 2010).

Since each rarity characteristic is important and cannot be used as a surrogate to infer the others, we chose to build an integrative measure of rarity by combining, into a single index, the three metrics (LA, GR, HB). Each metric was log-transformed to decrease the magnitude across observed values. To give the same weight to each metric, we standardized their values between 0 and 1 by dividing them by the respective maximum value observed over all species into each dataset. To take into account the degree of dependence between the three metrics, we down-weighted each one by its correlation with the two others (adapted from Kark *et al.* 2002). The rarity index for a species i (RI_i) is thus calculated as:

$$RI_i = [(LA_i \times w_{la}) + (GR_i \times w_{gr}) + (HB_i \times w_{hb})] / (w_{la} + w_{gr} + w_{hb})$$

where w_{la} , w_{gr} , and w_{hb} are the weighting parameters that represent the degree of independence of each rarity metric to the others. For instance, the weighting parameter for rarity in terms of local abundance w_{la} is calculated as:

$$w_{la} = 1/2 + [(1 - |r_{lagr}| / 2) + (1 - |r_{lahb}| / 2)]$$

where r_{lagr} is the Pearson’s correlation coefficient between local abundance and geographic range and r_{lahb} is the Pearson’s correlation coefficient between local abundance and habitat

breadth.

Since the metric of each characteristic scales between 0 and 1, and their weighted values are relativized by the sum of the weighting parameters, RI_i also varies between 0 (the potential value reached by the rarest species) and 1 (the potential value reached by the commonest species).

Functional structure of species assemblages

For each taxonomic group we first computed the functional distance between each pair of species. All traits were continuous for trees, so we computed the Euclidean distance on the scaled and centered trait values. Functional traits were not all continuous for fishes and birds (see Appendix S2), so we used the Gower distance which allows considering different types of traits while giving the same weight to each of them (Villéger *et al.* 2008). We then ran a Principal Coordinate Analysis (PCoA) on each functional distance matrix to build a multidimensional functional space and estimate the different functional facets of assemblage structure (Mouillot *et al.* 2013b). For each taxonomic group, the number of dimensions considered for further analyses was a trade-off between computation time and quality of the functional space (i.e. Mantel correlations between the initial distance and the Euclidean distance in the functional space). We kept the first four (Mantel $r = 0.91$), nine ($r = 0.98$), and five ($r = 0.98$) PCoA axes for fishes, trees and birds, respectively. A sensitivity analysis indicated that adding or removing one axis to compute the functional spaces did not affect the results (see Appendix S3).

We used three complementary indices to quantitatively describe the functional structure of assemblages: functional richness (FRic), functional specialization (FSpe), and functional originality (FOri). FRic is the volume of the functional space filled by all species within the assemblage indicating the range of trait combinations (Villéger *et al.* 2008; Fig. 1). We standardized FRic values by expressing them as a percentage of the volume filled by the pool of species in each dataset. FSpe represents the distinctiveness of species functional traits in the assemblage (Bellwood *et al.* 2006; Fig. 1). FSpe is expressed as the mean Euclidean distance between each species and the mean position of all species in the functional space. FOri reflects the degree of uniqueness (i.e. the opposite of redundancy) of species traits in the assemblage (Mouillot *et al.* 2013b; Fig. 1). FOri is expressed as the mean distance between each species and its nearest neighbor in the functional space. The raw values of FSpe and

FOri were standardized between 0 and 1 by dividing them, respectively, by the maximum distance to the barycenter and by the maximum nearest-neighbor distance observed over all species present in each dataset (Mouillot *et al.* 2013b). Since none of the rarity metrics was taken into account in the calculation of the functional indices, there was no circularity in the subsequent analyzes.

Scenarios of species loss

To assess the influence of rare vs. common species on the FS of assemblages we considered 10 classes of commonness, each containing 10% of the total number of species into each dataset ($S_{0.1}$), and we computed the three FS indices for each class. To test whether observed facet values in each class were higher or lower than expected by chance, we ran a null model where we computed the indices with a set of $S_{0.1}$ species randomly sampled in the pool (1,000 times without replacement). In order to assess the change in FS along the rarity-commonness gradient we performed ordinary least square regressions across classes.

To assess the consequences of potential extinctions on the FS of each of the three regional assemblages, we simulated a set of species-loss scenarios. We first sequentially removed species from each regional assemblage from the rarest to the commonest and we computed the three FS indices at each step. We compared the values obtained under this scenario with the ones obtained from a scenario simulating a sequential species loss from the commonest to the rarest and from a scenario simulating a random sequential extinction (1,000 times). Because the 22 rarest species of trees have an equal *RI* value, we randomized their rank 100 times and used the median value of FS for each deletion step.

Extinctions are rarely reported at the regional or global scale, whereas local extirpations are more frequent (Olden *et al.* 2008). Moreover, regional extinction does not directly bring information on the response of local FS to local species extirpation. To assess the consequences of potential species extirpations on local FS, we defined levels of biodiversity erosion for each local assemblage (from 10 to 90%, nine steps of 10%). Species removals, and subsequent computation of FS indices, were carried out following three different scenarios: rarest species lost first; commonest species lost first; and random loss of species (1,000 times). We then implemented a Friedman paired test (non-parametric analogous of repeated measures ANOVA) to compare the three scenarios. This allows removing the effects of local specificities (e.g. species richness) on FS while comparing the scenarios. When the remaining

number of species after species removal was lower than the number of functional dimensions, we excluded that local assemblage from the analysis (see final sample sizes in Table S1).

All computations were carried out using R software (R Core Team 2013), and a list of the main functions used with the respective packages is provided in Table S2.

RESULTS

At the regional scale, the 10% rarest species had higher functional richness (FRic), specialization (FSpe) and originality (FOri) values than expected by chance, while the 10% commonest species had values lower than expected by chance for fishes and birds and close to null expectations for trees (Fig. 2; see Figs. S2-4). A decreasing trend of FS indices from the rarest to the commonest sets of species was detected (Fig. 2).

Simulations of species removal from regional pools showed a consistent and significant pattern of faster decrease of FRic when species were lost from the rarest to the commonest compared to a random species loss (Fig. 3). For example, losing the 20% rarest species of fishes and trees led to a supplemental loss of, respectively, 7.2 and 9% of regional FRic when compared to a random species loss. For birds, the impact of rare species loss is even more critical, with the extinction of the 20% rarest species inducing an extra decrease of 28.3% for FRic compared to a random loss (Fig. 3). The extinction of the rarest species also led to a decrease of mean functional specialization and originality for the three taxonomic groups (Fig. 3). Conversely, when commonest species were removed in each of the three datasets, a general trend of increasing FSpe and FOri was observed (Fig. 3).

At the local scale, the loss of the rarest species also induced a severe decrease of FS indices. The erosion of FRic when the rarest species were removed was significantly higher than in the random loss scenario for all three groups (Fig. 4). Conversely, FRic generally dropped less than expected by chance when common species were firstly removed (Fig. 4). Similarly to the regional scale, the impact of rare species loss on local FRic was more pronounced for bird assemblages. FSpe of local assemblages decreased more than expected when the rarest species were firstly removed for the three study cases (Fig. 4). Local FOri of tree and bird assemblages decreased more than expected when the rarest species were firstly removed, whereas it increased when commonest species were lost first (Fig. 4). For local assemblages

of stream fishes, FOr values did not differ from null model expectations when the top 50% rarest species were removed first, but they were significantly higher than expected when the top 50% commonest species were removed first (Fig. 4).

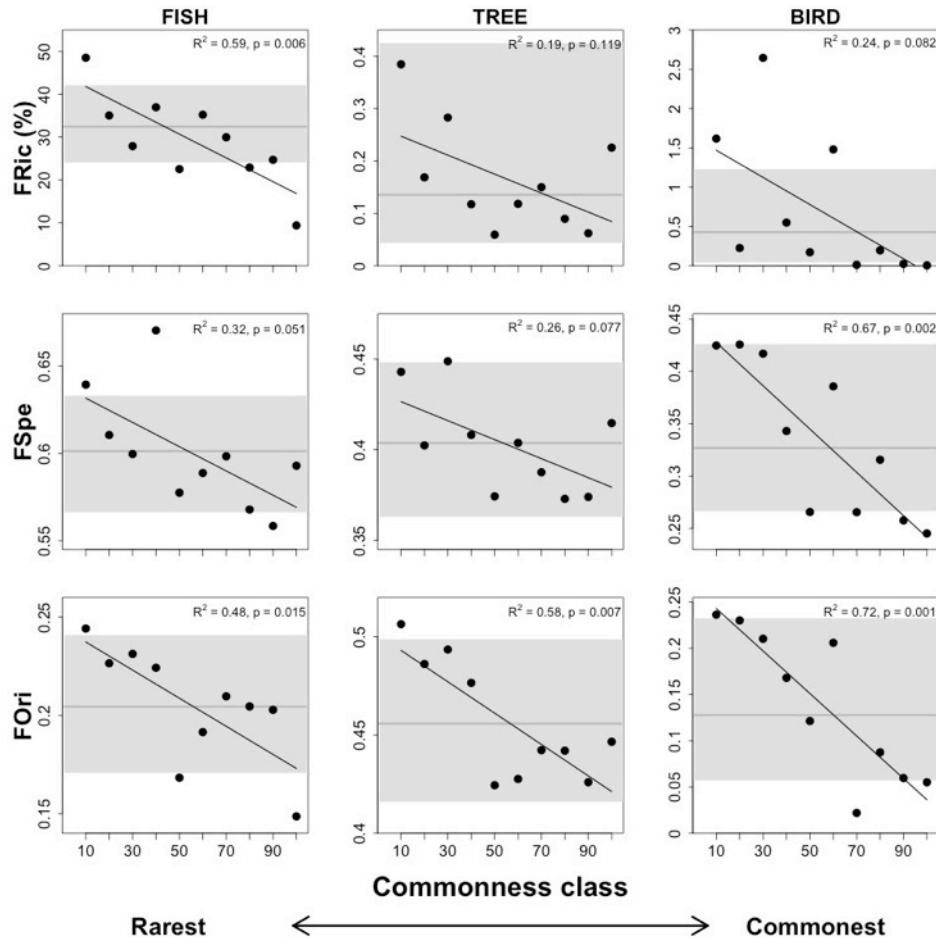


Figure 2 Functional structure (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOr) supported by rare and common species of three tropical species assemblages: stream fishes from the Brazilian Amazon, rainforest trees from French Guiana, and birds from the Australian Wet Tropics. Commonness classes contain 10% of the global pool of species (395 fishes, 262 trees, 86 birds) and are ordered from the rarest to the commonest species. Gray lines and shaded areas indicate the median and the quantiles 5 – 95% obtained by randomization. Black lines represent ordinary least square regressions.

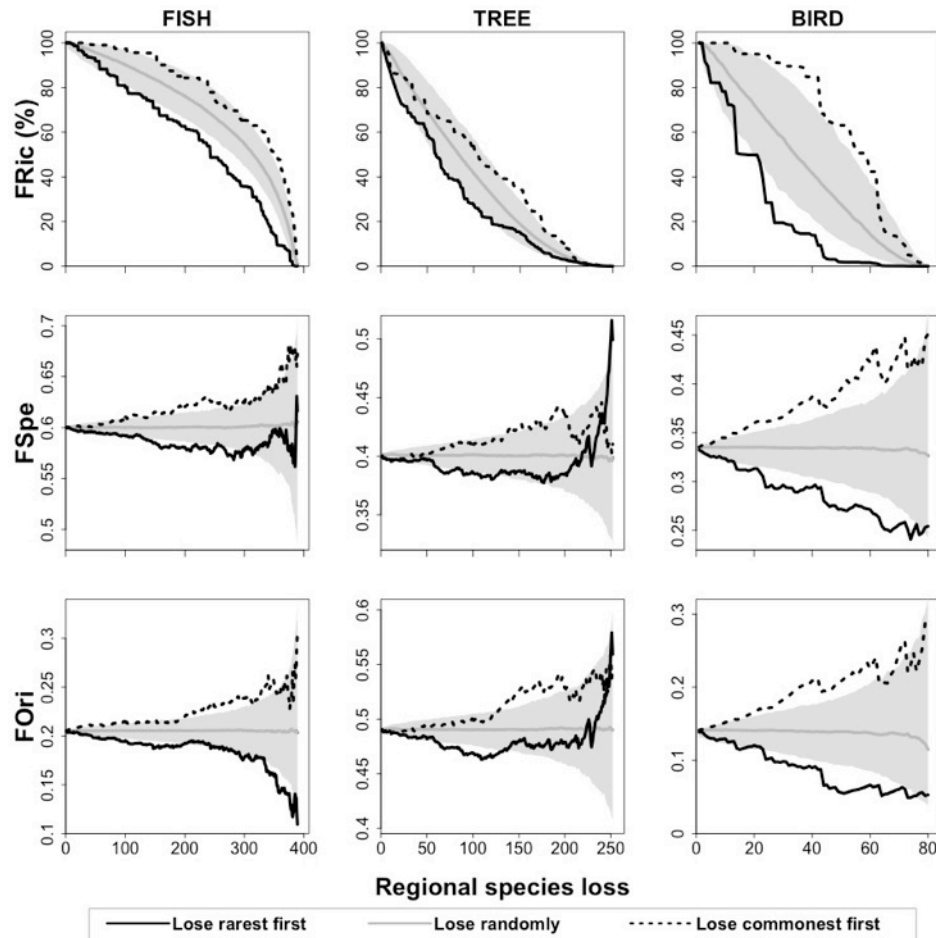


Figure 3 Impact of regional species extinction of the rarest species on the functional structure (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) of three tropical assemblages: stream fishes from the Brazilian Amazon, rainforest trees from French Guiana, and birds from the Australian Wet Tropics. Rarest species erosion is compared to the opposite situation where commonest species are lost first and with a random species erosion (gray line indicates the median of this scenario among the 1,000 replicates and the 95% confidence interval is represented as the shaded area).

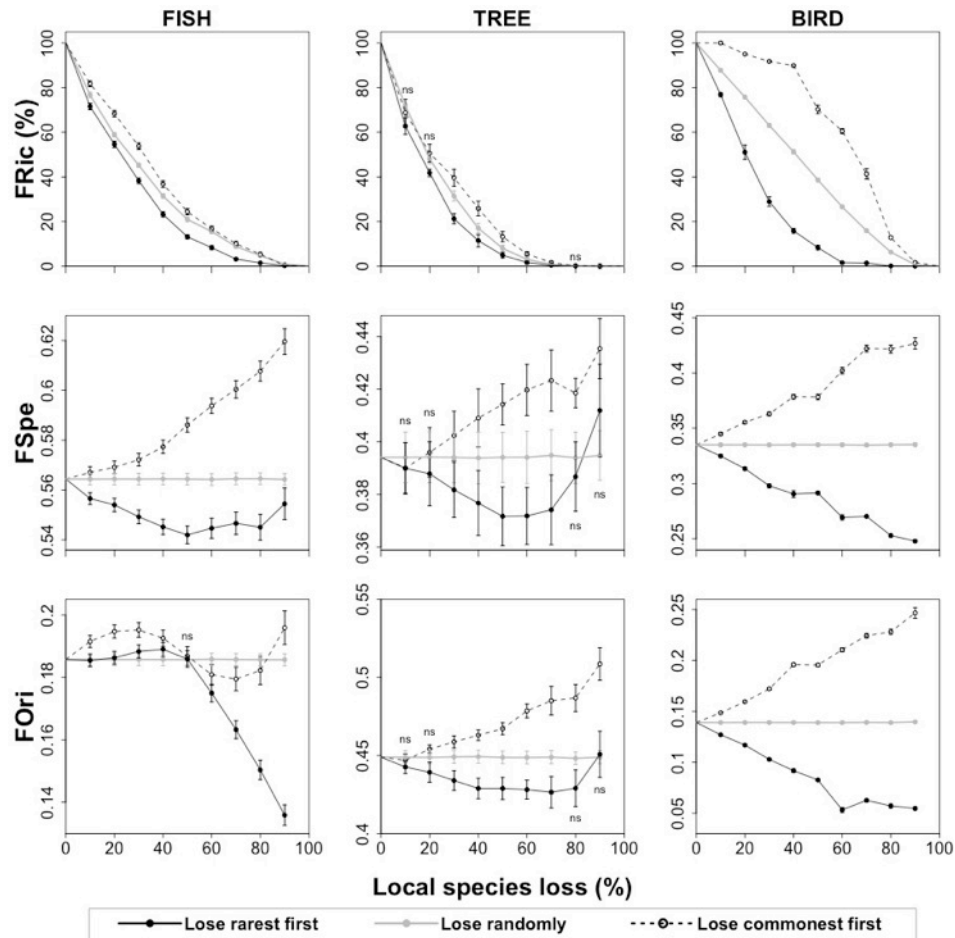


Figure 4 Impact of local species extinction on the functional structure – FS (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOrl) of local assemblages of stream fishes from the Brazilian Amazon, rainforest trees from French Guiana, and birds from the Australian Wet Tropics. For computations of FS indices, 10 to 90% of the species of each local assemblage were removed according to three different scenarios: lose the rarest species first; lose the commonest species first; lose species randomly. Dots and vertical bars (when bigger than dots) represent mean values and standard error at the species-removal level among all local assemblages. ‘ns’ indicates similarity ($p > 0.05$) between scenarios for a given level of species removal (see Friedman paired test and sample sizes in Table S1).

DISCUSSION

All our scenarios of species loss demonstrate a disproportionate impact of rare species extinction on the functional structure of tropical assemblages compared to a random loss, both at local and regional scales. Losing rare species would reduce the functional richness, specialization and originality of assemblages more than expected under a random loss of species. The generality of these findings is strengthened by the similar patterns observed among three taxonomic groups highly distinct in terms of evolutionary history, biology and

habitat. Stream fishes are distributed across complex dendritic river networks, with dispersal constrained by non-floodable terrains while local abundances are regulated by hydrological dynamics (Jackson *et al.* 2001). Bird distributions are more homogeneous across the landscape, with occurrences and local abundances usually determined by phytophysiognomic and climatic regional characteristics (Williams & Middleton 2008). On the other extreme, trees are sessile autotrophic organisms whose distribution patterns strongly depend on passive dispersion (Condit *et al.* 2002) and on climatic and edaphic factors (Fortunel *et al.* 2014). Despite these particularities, we found strong convergent patterns of rare species over-contributing to assemblage functional structure across all three groups.

Using a single and individual species-based functional index, Mouillot *et al.* (2013a) showed that in regional species pools the most distinct combinations of traits are supported by rare species but that, at the same time, many rare species support common traits and thus redundant functions. On the balance, the impact of rare loss on assemblage functional structure remained unknown. Scaling up at the assemblage level and using a multifaceted framework, we demonstrated that beyond supporting the most unusual traits, rare species over-contribute to the functional structure of species assemblages in several ways, as illustrated by a closer examination of their positions in the functional space (Fig. 5). For instance, the southern cassowary *Casuarius casuarius* (Casuariidae), ranked within the top 16% rarest species and listed as vulnerable by the IUCN (2014), strongly contributes to the functional structure of bird assemblages in the Australian Wet Tropics because of its high functional specialization and originality (Fig. 5). This species is the only remaining large-bodied (males weighing up to 50kg and females up to 76kg) plant disperser on long distances in Australian tropical rainforests (Westcott *et al.* 2005). Losing *C. casuarius* should thus affect plant population dynamics across the landscape, particularly for large-seeded species.

The rainforest trees *Brosimum acutifolium* (Moraceae) and *Protium giganteum* (Burseraceae), both within the top 20% rarest species in French Guiana, are placed relatively isolated (i.e. contributing to the FOr_i of assemblages) and at opposite extremes in the functional space (Fig. 5). The former is characterized by having dense wood and high specific leaf area with milky latex and dense hairs on leaves, which is typically associated with exceptional defense capacity against herbivores and fungal pathogens (Chave *et al.* 2009). On the other functional extreme, *P. giganteum* holds high values of laminar and trunk bark thickness, which insures protection against the increasing frequency and intensity of wildfires that may occur in the

region (Brando *et al.* 2012). The asynchrony of species responses to environmental fluctuations and to perturbations is an important mechanism through which biodiversity can stabilize ecosystem properties (Loreau & de Mazancourt 2013). In this context, maintaining rare species and the consequent high diversity of traits within assemblages may provide resistance and resilience to a variety of disturbances in changing landscapes.

Regarding the stream fish assemblages, rare species tend to be placed on the edge of the functional space, increasing functional richness and specialization. For instance, the vampire catfish *Paravandellia* sp. (Trichomycteridae), ranked within the top 2% rarest species (Fig. 5), has a very particular oral apparatus to feed on blood from other small-bodied fishes (Zuanon & Sazima 2005), being one of the few hematophagous species recorded for small Amazonian streams. The poeciliid *Fluviophylax simplex*, ranked within the top 5% rarest species (Fig. 5), is a miniature fish with highly specialized morphology (e.g. superior-oriented mouth and extremely large eyes) allowing to exclusively feed on fine particulate detritus and very small preys associated to the water-air interface (i.e. neustophagia). Beyond individual species, some rare functional entities have critical functions in aquatic systems. That is the case of periphyton-grazing fishes, which have restricted geographic ranges and are often found in low local abundances in small Amazonian forest streams (13 species among the top 20% rarest; Fig. 5). These species use particular traits to directly exploit the periphyton, being the only fish group responsible for the early incorporation of autotrophic carbon along the fluvial continuum (M. Anjos, personal communication). Therefore, more than taxonomic, aesthetic, or ethical values, extirpating rare species may represent the loss of irreplaceable functions within assemblages, potentially disrupting refined ecological interactions among species, eradicating highly specialized forms of resource utilization and affecting several ecosystem processes.

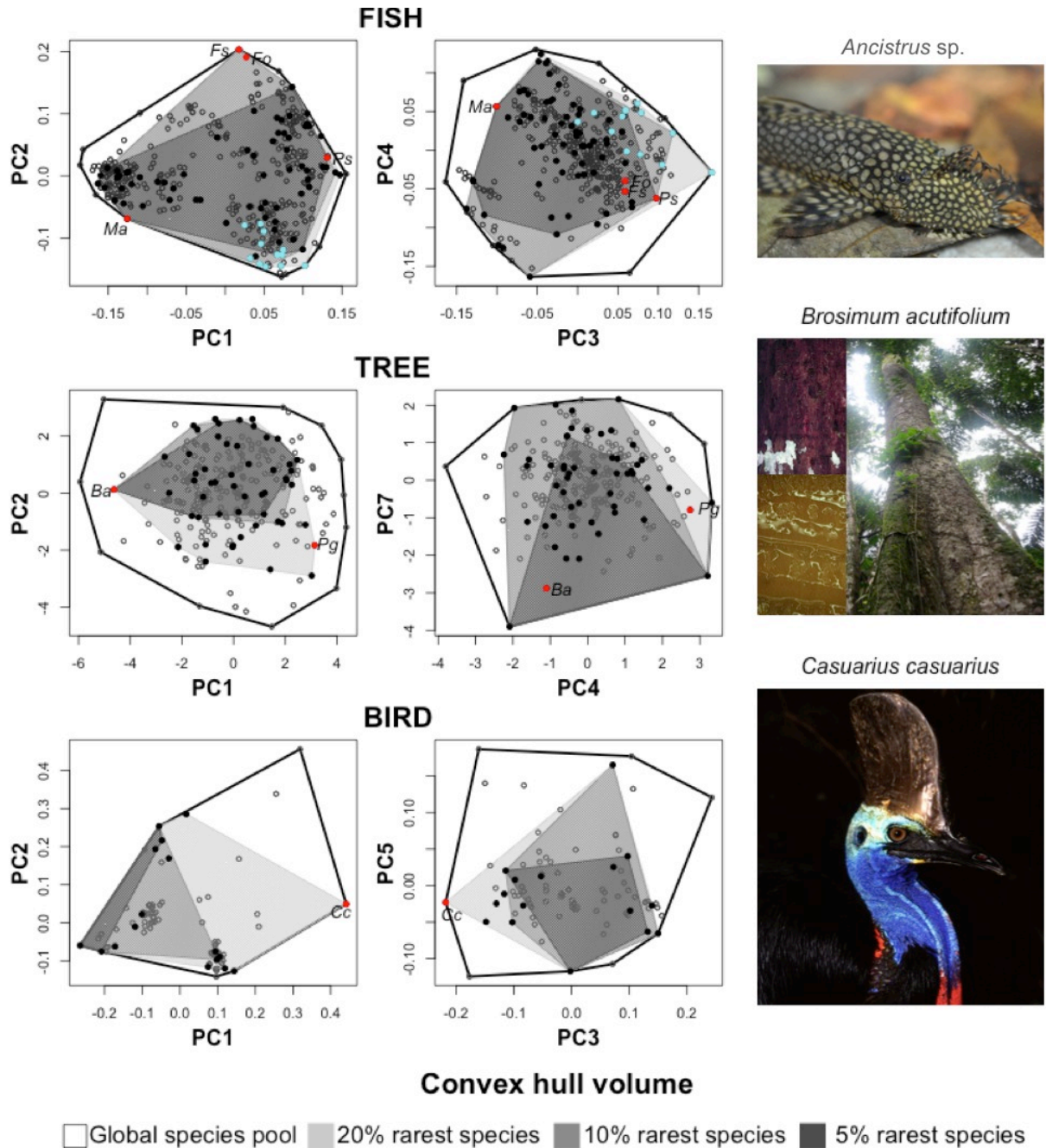


Figure 5 Multidimensional functional spaces built with the species pool of three tropical assemblages: stream fishes from the Brazilian Amazon (395 species), rainforest trees from French Guiana (262), and birds from the Australian Wet Tropics (86). Each plot represents two axes (PC) of the functional space where species are plotted with circles according to their respective trait values. The 20% rarest species are filled with black. Volumes filled by the 5, 10, and 20% rarest species are illustrated as the nested grey areas. Blue points on top panels are periphyton-grazing fishes, illustrated by the loricariid *Ancistrus* sp.. Red points represent species cited in the Discussion section (Ps: *Paravandellia* sp.; Fs: *Fluviphylax simplex*; Fo: *Fluviphylax obscurus*; Ma: *Myloplus asterias*; Ba: *Brosimum acutifolium*; Pg: *Protium giganteum*; Cc: *Casuarius casuarius*).

Evidences of significant influence of rare species on local ecological processes are still sparse but Lyons & Schwartz (2001) demonstrated the complementarity of less common grass species improving resistance to invasions in meadow systems. Power *et al.* (1996) reviewed several examples of top predators exerting functional impacts disproportional to their abundances (i.e. keystone species). Bracken & Low (2012) recorded large and disproportionate bottom-up effects of rare (i.e. cornerstone species) seaweeds and sessile invertebrates on consumers from rocky shore communities. Nevertheless, most of the research on these relationships has so far examined individual processes even though ecosystem functioning relies on many processes that often require multiple ecological roles to be achieved (Hector & Bagchi 2007) across many environmental conditions (Isbell *et al.* 2011). This multifunctionality of ecosystems is more strongly predicted by the functional structure of assemblages than by their species richness (Mouillot *et al.* 2011), suggesting that the loss of rare species and subsequent disruption of functional structure may result in drastic impacts on the provisioning of ecosystem goods and services.

We demonstrated that losing rare species negatively over-influenced assemblage functional structure not only at the local scale but also at the regional scale. Biodiversity can provide insurance for ecosystem functioning across several spatial scales producing alpha, beta and gamma diversity-stability relationships (Wang & Loreau 2014). As a consequence, losing species may impair ecosystem stability and functioning at large spatial scales by reducing the capacity of connected systems to share or replace potential key functions (i.e. insurance effect). This is particularly important for management decisions, which are often made at the landscape scale (Wang & Loreau 2014). Given that this spatial biodiversity-stability relationship is primarily driven by differences in the fundamental niches and complementarity of the species (Loreau & Hector 2001), keeping the pool of traits and the functional structure of regional assemblages is critical to maintain the functional insurance within and across ecosystems. In this sense, our results suggest that special attention should be given to rare species protection given the low functional redundancy and high functional richness they support within assemblages.

In addition to the implications for biodiversity conservation, our findings bring interesting insights on the community ecology theory, particularly regarding the opposing sets of hypotheses proposed to explain the assembly of rare vs. common species into communities. Neutral models assume ecological equivalence among species, with their abundances mainly

driven by dispersal limitation and demographic stochasticity (Hubbell 2001). In contrast, niche differentiation hypotheses postulate that species rarity and commonness will be better explained by differences in functional traits and their interaction with prevailing environmental conditions (Gaston 2011). Under this latter assumption, rare species should be ecologically distant from common species and from each other, with the mechanism of resource partitioning mainly driving community assembly (see Mi *et al.* 2012 for an example of how these opposing paradigms were tested drawing upon rare species contribution to the phylogenetic diversity of communities). Although our study has not been designed to test community assembly, the high functional specialization and originality supported by rare species may indicate that niche differentiation mechanisms are important determinants in tropical assemblages. Particularly for tree assemblages, however, the relatively smaller difference in the contribution of the top 20% rarest and commonest species may suggest that neutral processes are also important. Further conclusions are out of the scope of this study, but explicit comparison of causal factors on mobile vs. sessile organisms (i.e. fixed number of individuals within a restrict space and establishment success more affected by passive-dispersion colonization and random births; Ricklefs 2003) community assembly based on a functional trait approach is a promising step forward to better understand species distribution in tropical ecosystems.

Although broad in scale, our study includes some limitations. Firstly, we assume that traits are relevant proxies for species roles while this is sometimes not so straightforward (Kraft *et al.* 2015). In reality, traits certainly matter for defining functions, but some functions are still ignored because corresponding traits cannot be easily measured (e.g. ecophysiological characteristics in animals). Also, we did not distinguish naturally rare from wanderer species across the sampling areas. For example, the herbivorous fish *Myloplus asterias* (Serrasalminidae) has extreme traits related to teeth shape and body depth among the fish species pool and was ranked within the top 2% rarest species (Fig. 5). However, it is a typical inhabitant of Amazon's large lowland rivers and may only occasionally invade headwater streams, being its potential functions to the studied ecosystem contestable. Finally, we recognize that, particularly for tree species, using additional secondary data to define their geographic range would improve the strength of our rarity vs. commonness estimates. However, we believe this will not change our main conclusions, firstly because the general patterns found across species loss simulations converge with the other two taxonomic groups. Moreover, for several species, we found consistence between the rarity ranking from our

estimates and from a broader published assessment of Amazon tree distribution (i.e. ter Steege *et al.* 2013).

Given the operational difficulties involving the study of rare species (e.g. poor ecological knowledge and accessibility), they have frequently been neglected in community ecology and in experimental tests of the effects of biodiversity on ecosystem functioning (Lyons *et al.* 2005). According to the ‘commonness-dominant’ paradigm, the focus on the common species is also justified because they often account for the major overall biomass and energy use in a community, supposedly playing a stronger role in the structure and functioning of ecosystems than do rare ones (Gaston 2011). However, our results indicate that this overlooked attention on the rare species can be a misjudgment, since they are irreplaceable components of the functional structure of assemblages. Moreover, the loss of rare species could have deep impacts on community functioning if they exhibit compensatory growth to common species declines or are favored by environmental changes (Jain *et al.* 2014). Tropical ecosystems are facing unprecedented levels of pressure from multiple sorts and scales. Our empirical knowledge on tropical biodiversity is still too limited to make robust predictions about its conservation value (Gardner *et al.* 2007). However, it is reasonable to assume that not just common and dominant species are functionally important. Rare species, that combine low local abundance, restricted geographic range and narrow habitat breadth, over-contribute to the functional structure of assemblages and have potentially critical roles to sustain the multifunctionality of ecosystems, justifying the application of the precautionary principle for the tropical biodiversity conservation.

ACKNOWLEDGEMENTS

We thank D. Bastos, L. Carvalho, F. Cabeceira, R. Júnior, and RAS Project for sharing part of the fish data. F. Guilhaumon, F. Leprieur, V. Parravicini and A. Escalas for helping with R-codes. N. Rabelo and S. Cunha for helping with ecomorphological analysis. B. Forsberg (PRONEX/FAPEAM) for fieldwork support. *Brosimum* pictures courtesy of M. Hopkins and R. Van Loon (CaminoVerde). F. Teresa, T. Oberdorff, C. Cornelius, S. Amadio, C. Deus and D. Kasper revised the manuscript. JZ received productivity grant from CNPq(#307464/2009-1). Research for trees was supported by NSF-DEB-0743103/0743800, INRA Package grant, and an "Investissement d’Avenir" grant managed by Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-25-01). This study is part of RPL PhD thesis, supported by

CNPq(#156915/2011-1) and CAPES(Science Without Borders - PDSE#1914-13-8). This is contribution #XX of the Projeto Igarapés.

REFERENCES

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., Dávila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V.A. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677–2688.

Baraloto, C., Molto, Q., Rabaud, S., Hérault, B., Valencia, R., Blanc, L., Fine, P.V.A. & Thompson, J. (2013) Rapid simultaneous estimation of aboveground biomass and tree diversity across Neotropical forests: a comparison of field inventory methods. *Biotropica*, **45**, 288–298.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.

Bellwood, D.R., Wainwright, P.C., Fulton, C.J. & Hoey, A.S. (2006) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B*, **273**, 101–107.

Bracken, M.E.S. & Low, N.H.N. (2012) Realistic losses of rare species disproportionately impact higher trophic levels. *Ecology Letters*, **15**, 461–467.

Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. & Putz, F.E. (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.

Brook, B.W., Bradshaw, C.J.A., Koh, L.P. & Sodhi, N.S. (2006) Momentum drives in the crash: mass extinction in the tropics. *Biotropica*, **38**, 302–305.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

- Condit, R., Pitman, N., Leigh Jr., E.G., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666–669.
- Davies, K.F., Margules, C.R. & Lawrence, J.F. (2004) A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology*, **85**, 265–271.
- Diáz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.
- Dolédec, S., Chessel, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.
- Fey, S.B., Siepielski, A.M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J.L., Huber, E.R., Fey, M.J., Catenazzi, A. & Carlson, S.M. (2015) Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences USA*, **112**, 1083–1088.
- Fortunel, C., Fine, P.V.A. & Baraloto, C. (2012) Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology*, **26**, 1153–1161.
- Fortunel, C., Paine, C.E.T., Fine, P.V.A., Kraft, N.J.B. & Baraloto, C. (2014) Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology*, **102**, 145–155.
- Gardner, T.A., Barlow, J., Parry, L.T.W. & Peres, C.A. (2007) Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica*, **39**, 25–30.
- Gaston, K.J. (1991) How large is a species' geographic range? *Oikos*, **61**, 434–438.
- Gaston, K.J. (2011) Common ecology. *Bioscience*, **61**, 354–362.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder

effects. *Journal of Ecology*, **86**, 902–910.

Harnik, P.G., Simpson, C. & Payne, L. (2012) Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society B*, **279**, 4969–4976.

Hector, A. & Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. *Nature*, **448**, 188–190.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

Hubbell, S.P. (2013) Tropical rain forest conservation and the twin challenges of diversity and rarity. *Ecology and Evolution*, **3**, 3263–3274.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S. & Loreau, M. (2011) High plant diversity is needed to maintain ecosystem services. *Nature*, **477**, 199–202.

IUCN (2014) IUCN red list of threatened species. Available at: [http:// www.iucnredlist.org](http://www.iucnredlist.org). Last accessed 25 June 2014.

Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. (2001) What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Science*, **58**, 157–170.

Jain, M., Flynn, D.F.B., Prager, C.M., Hart, G.M., DeVan, C.M., Ahrestani, F.S., Palmer, M.I., Bunker, D.E., Knops, J.M.H., Jouseau, C.F. & Naeem, S. (2014) The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and

possible ecosystem function in tall-grass prairies. *Ecology and Evolution*, **4**, 104–112.

Kark, S., Mukerji, T., Safriel, U.N., Noy-Meir, I., Nissani, R. & Darvasi, A. (2002) Peak morphological diversity in an ecotone unveiled in the chukar partridge by a novel estimator in a dependent sample (EDS). *Journal of Animal Ecology*, **71**, 1015–1029.

Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015) Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences USA*, **112**, 797–802.

Lavergne, S., Thuiller, W., Molina, J. & Debussche, M. (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. *Journal of Biogeography*, **32**, 799–811.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.

Loreau, M. & de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters*, **16**, 106–115.

Lyons, K.G. & Schwartz, M. (2001) Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters*, **4**, 358–365.

Lyons, K.G., Brigham, C.A., Traut, B.H. & Schwartz, M.W. (2005) Rare species and ecosystem functioning. *Conservation Biology*, **19**, 1019–1024.

Magurran, A.E. (2009) Threats to freshwater fish. *Science*, **325**, 1215–1216.

Mi, X., Swenson, N.G., Valencia, R., Kress, W.J., Erickson, D.L., Pérez, A.J., Ren, H., Su, S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Ye, W., Cao, M., Suresh, H.S., Dattaraja, H.S., Sukumar, R. & Ma, K. (2012) The contribution of rare species to community phylogenetic diversity across a global network of forest plots. *The American Naturalist*, **180**, E17–E30.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason, N.W.H. (2011) Functional

structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, **6**, e17476.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J. & Thuiller, W. (2013a) Rare species support vulnerable functions in high-diversity ecosystems. *PLOS Biology*, **11**, e1001569.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013b) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167–177.

Naeem, S., Duffy, J.E & Zavaleta, E. (2012) The functions of biological diversity in an age of extinction. *Science*, **336**, 1401–1406.

Olden, J.D., Poff, N.L. & Bestgen, K.R. (2008) Traits synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology*, **89**, 847–856.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T. (1996) Challenges in the quest for keystones. *Bioscience*, **46**, 609–620.

Purvis, A., Agapow, P.M., Gittleman, J.C. & Mace, G.M. (2000) Non-random extinction and the loss of evolutionary history. *Science*, **288**, 328–330.

R Core Team (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Available at: [http:// www.R-project.org](http://www.R-project.org). Last accessed 17 June 2014.

Rabinowitz, D. (1981) Seven forms of rarity. *The biological aspects of rare plant conservation* (ed. by J. Synge), pp. 205–217. Wiley, New York.

Ricklefs, R. (2003) A comment on Hubbell's zero-sum ecological drift model. *Oikos*, **100**, 185–192.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, **22**, 140–150.

ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C.V., Magnusson, W.E., Molino, J.F., Monteagudo, A., Núñez Vargas, P., Montero, J.C., Feldpausch, T.R., Coronado, E.N.H., Killeen, T.J., Mostacedo, B., Vasquez, R., Assis, R.L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W.F., Laurance, S.G.W., Marimon, B.S., Marimon, B.H., Vieira I.C.G., Amaral, I.L., Brienen, R., Castellanos, H., López D.C., Duivenvoorden, J.F., Mogollón, H.F., Matos, F.D.A., Dávila, N., García-Villacorta, R., Diaz P.R.S., Costa, F., Emilio, T., Levis, C., Schiatti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A.J.D., Piedade, M.T., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P.V.A., Peres, C.A., Toledo, M., Aymard, C.G.A., Baker, T.R., Cerón, C., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Stropp, J., Zartman, C.E., Daly, D., Neill, D., Silveira, M., Paredes, M.R., Chave, J., Lima Filho, D.A., Jørgensen, P.M., Fuentes, A., Schöngart, J., Valverde, F.C., Di Fiore, A., Jimenez, E.M., Mora, M.C.P., Phillips, J.F., Rivas, G., van Andel, T.R., von Hildebrand, P., Hoffman, B., Zent, E.L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A.R., Silva, N., Vos, V., Zent, S., Oliveira, A.A., Schutz, A.C., Gonzales, T., Nascimento, M.T., Ramirez-Angulo, H., Sierra, R., Tirado, M., Medina, M.N.U., van der Heijden, G., Vela, C.I.A., Torre, E.V., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Giraldo, L.E.U., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Cuenca, W.P., Pauletto, D., Sandoval, E.V., Gamarra, L.V., Dexter, K.G., Feeley, K., Lopez-Gonzalez, G. & Silman, M.R. (2013) Hyperdominance in the Amazonian tree flora. *Science*, **342**, 1243092.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.

Villéger, S., Miranda, J.R., Hernandez, D.F. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, **20**, 1512–1522.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of

Earth's ecosystems. *Science*, **277**, 494–499.

Wang, S. & Loreau, M. (2014) Ecosystem stability in space: α , β and γ variability. *Ecology Letters*, **17**, 891–901.

Westcott, D.A., Bentrupperbäumer, J., Bradford, M.G. & McKeown, A. (2005) Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57–67.

Williams, S.E. & Middleton, J. (2008) Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions*, **14**, 69–77.

Williams, S.E., Williams, Y.M., VanDerWal, J., Isaac, J., Shoo, L.P. & Johnson, C.N. (2009) Ecological specialization and population size in a biodiversity hotspot: how rare species avoid extinction. *Proceedings of the National Academy of Sciences USA*, **106**, 19737–19741.

Williams, S.E., VanDerWal, J., Isaac, J., Shoo, L.P., Storlie, C., Fox, S., Bolitho, E.E., Moritz, C., Hoskin, C.J. & Williams, Y.M. (2010) Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology*, **91**, 2493.

Zuanon, J. & Sazima, I. (2005) Free meals on long-distance cruisers: the vampire fish rides giant catfishes in the Amazon. *Biota Neotropica*, **5**, 109–114.

SUPPORTING INFORMATION

Rare species over-contribute to the functional structure of species assemblages

Appendix S1. Local habitat assessment

Fishes

A set of 15 environmental parameters describing stream channel structure, substrate and water quality was taken at each sampled site (320 streams) in the Brazilian Amazon (Table A1.1; Fig. A1.1). These variables were used to estimate the habitat breadth of each fish species in this study. Detailed description of measurements is found in Mendonça *et al.* (2005).

Table A1.1: Environmental parameters measured in each of the 320 streams sampled for fishes in the Brazilian Amazon.

Group	Variable	Unit	Mean	Min	Max
Channel structure	Mean width	m	2.28	0.44	10.78
	Mean depth	m	0.21	0.02	0.87
	Mean current velocity	cm s ⁻¹	18.56	0.00	100.68
Substrate	Sand	%	24.99	0.00	88.89
	Clay	%	5.76	0.00	91.43
	Coarse litter	%	33.48	0.00	97.22
	Organic silt	%	12.40	0.00	64.44
	Trunk	%	5.89	0.00	38.00
	Fine roots	%	11.69	0.00	58.33
	Macrophytes	%	1.24	0.00	75.24
	Gravel	%	2.60	0.00	56.19
	Boulder	%	1.97	0.00	88.89
Water quality	Temperature	° C	24.82	20.40	29.40
	O ₂	mg L ⁻¹	5.18	0.62	8.81
	pH	N/A	5.00	3.02	8.70

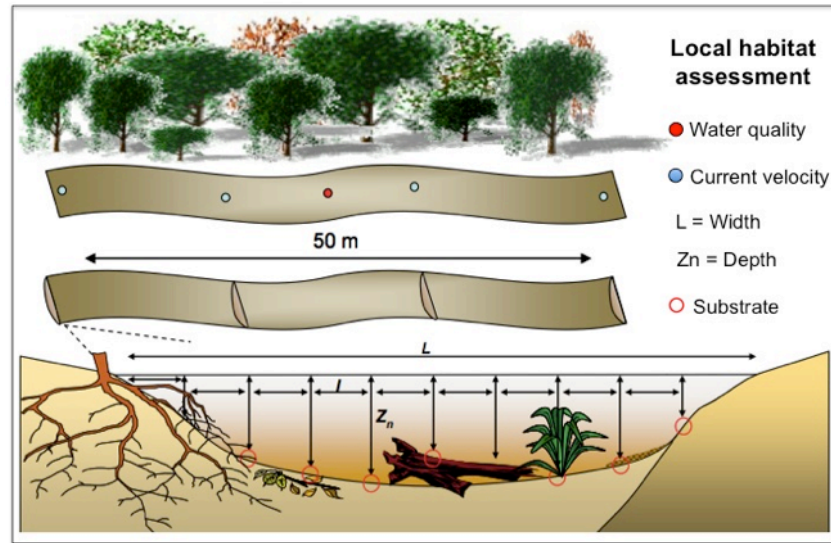


Figure A1.1: Schema of local habitat assessment for Amazonian fishes showing where each environmental parameter was measured at the streams.

Trees

A set of 14 environmental parameters describing climate and soil characteristics was taken at each sampled site (36 forest plots) in Amazon rainforests from French Guiana (Table A1.2). These variables were used to estimate the habitat breadth of each tree species in this study. Detailed description of measurements is found in Baraloto *et al.* (2010a, b, 2013) and Fortunel *et al.* (2012, 2014).

Table A1.2: Environmental parameters measured in each of the 36 rainforest plots sampled for trees in French Guiana.

Group	Variable	Unit	Mean	Min	Max
Climate	Rainfall	mm yr ⁻¹	3208.53	2471.00	4421.00
	Dry season index	days	27.91	23.70	36.80
Soil	N	%	0.21	0.02	0.76
	C	%	3.08	0.51	13.62
	C : N	N/A	16.40	1.94	26.41
	NO ₃ – N	ppm	8.14	0.10	55.22
	Olsen P	ppm	3.19	1.00	12.20
	K	mEq/100g	0.09	0.01	0.22
	Na	mEq/100g	0.06	0.01	0.16
	Ca	mEq/100g	0.41	0.03	4.15
	Mg	mEq/100g	0.36	0.06	1.83
	Sand	%	72.07	18.00	99.00
Silt	%	8.42	1.00	36.00	
Clay	%	19.54	0.43	69.00	

Appendix S2. Functional trait assessment

Fishes

We conducted an ecomorphological analysis to evaluate functional structure in fish assemblages by characterizing species for three key functions: food acquisition, locomotion, and habitat preferences. Body mass and morphometric measures (Fig. A2.1) were taken on 1,965 specimens from 395 species (up to 12 individuals per species), and then combined into 15 ecomorphological traits (Table A2.1). These traits, except the log-transformed mass, are expressed as unitless ratios, reducing body-size effects. We also assessed the number and shape of teeth and gill rakers on one individual per species. These 18 functional traits are commonly used in functional and ecomorphology studies (Table A2.1).

Specimens were weighted using electronic balance (0.001 g). Body width, mouth width, mouth depth, snout length and protrusion length were measured using digital caliper (0.1 mm). The other morphological measures were taken by the use of digital pictures analyzed in Image J software (0.1 mm). The evaluation of gill-raker and teeth characteristics was made under binocular microscope.

Although this standard protocol was designed to cover a broad range of morphologies among fish groups (Villéger *et al.* 2010), we had to use some particular conventions. Synbranchiformes and Gymnotiformes (except Apterontidae) have no caudal fin, so the *Aspect ratio of the caudal fin*, *Fins surface ratio*, and *Caudal peduncle throttling* were fixed to 0. Synbranchiformes also have no pectoral fins, so *Pectoral fin position*, *Aspect ratio of the pectoral fin*, and *Fins surface to body size ratio* were fixed to 0.

Voucher specimens from all species are deposited in the fish collection of National Institute for Amazonian Research – INPA, Manaus, Brazil.

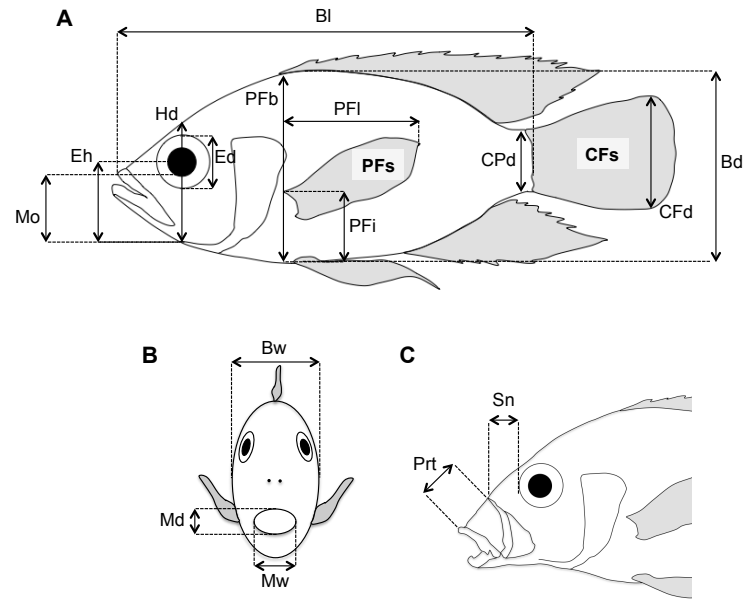


Figure A2.1: Morphological traits measured for fish on digital pictures (A): *Bd* body depth, *CPd* caudal-peduncle minimal depth, *CFd* caudal-fin depth, *CFs* caudal-fin surface, *PFI* distance between the insertion of pectoral fin to the bottom of the body, *PFI* pectoral-fin length, *PFI* pectoral-fin surface, *Hd* head depth along the vertical axis of the eye, *Ed* eye diameter, *Eh* distance between the center of the eye to the bottom of the head, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis; and with digital caliper (B, C): *Bw* body width, *Md* mouth depth, *Mw* mouth width, *Sn* snout length, *Prt* protrusion length.

Table A2.1: List of the 18 functional traits measured for stream fishes from the Brazilian Amazon. Codes for morphological measures are showed in Fig. A2.1.

Functional trait	Calculation/ Class	Nature	Ecological meaning	References
Teeth shape	Absent	Nominal	Nature of food items captured and feeding method	adapted from Gatz (1979); Keenleyside (1979); Sazima (1986)
	Canine			
	Comb-shaped			
	Conic			
	Incisiform			
	Molariform			
	Aliasing multicuspid			
	Spoon-shaped			
Number of teeth	Tricuspid	Continuous	Nature of food items captured and feeding method	adapted from Gatz (1979)
	Viliform			
	Mean number of teeth between upper and lower jaws			
Gill-raker shape	Absent	Ordinal	Filtering ability and gill protection	adapted from Sibbing & Nagelkerke (2001)
	Short/ sparse			
	Intermediate			
	Long/ numerous			

Protrusion length	$\frac{Prt}{Sn}$	Continuous	Nature of food items captured and feeding method	adapted from Gatz (1979)
Oral-gape surface	$\frac{Mw \times Md}{Bw \times Bd}$	Continuous	Nature/Size of food items captured	adapted from Karpouzi & Stergiou (2003)
Oral-gape shape	$\frac{Md}{Mw}$	Continuous	Method to capture food items	Karpouzi & Stergiou (2003)
Oral-gape position	$\frac{Mo}{Hd}$	Continuous	Feeding method in the water column	adapted from Sibbing & Nagelkerke (2001)
Eye size	$\frac{Ed}{Hd}$	Continuous	Prey detection	adapted from Boyle & Horn (2006)
Eye position	$\frac{Eh}{Hd}$	Continuous	Vertical position in the water column	Gatz (1979)
Body transversal shape	$\frac{Bd}{Bw}$	Continuous	Vertical position in the water column and hydrodynamism	Sibbing & Nagelkerke (2001)
Body transversal surface	$\frac{\ln [(\frac{\pi}{4} \times Bw \times Bd) + 1]}{\ln (\text{Mass} + 1)}$	Continuous	Mass distribution along the body for hydrodynamism	Villéger <i>et al.</i> (2010)
Pectoral-fin position	$\frac{Pfi}{PFb}$	Continuous	Pectoral fin use for maneuverability	Dumay <i>et al.</i> (2004)
Aspect ratio of the pectoral fin	$\frac{Pfl^2}{PFs}$	Continuous	Pectoral fin use for propulsion	adapted from Fulton <i>et al.</i> (2001)
Caudal fin-peduncle depth ratio	$\frac{CFd}{CPd}$	Continuous	Caudal propulsion efficiency through reduction of drag	Webb (1984)
Aspect ratio of the caudal fin	$\frac{CFd^2}{CFs}$	Continuous	Caudal fin use for propulsion and/or direction	Webb (1984)
Fins surface ratio	$\frac{2 \times PFs}{CFs}$	Continuous	Main type of propulsion between caudal and pectoral fins	Villéger <i>et al.</i> (2010)
Fins surface to body size ratio	$\frac{(2 \times PFs) + CFs}{\frac{\pi}{4} \times Bw \times Bd}$	Continuous	Acceleration and/or maneuverability efficiency	Villéger <i>et al.</i> (2010)
Mass	$\log (\text{Mass} + 1)$	Continuous	Metabolism, endurance and swimming ability	Villéger <i>et al.</i> (2010)

Trees

We measured 15 leaf and wood traits (Table A2.2) for 262 tree species (one individual per species in each sampled plot). Palm species were excluded because of the unfeasibility to measure stem wood specific gravity. Detailed methods are found in Fortunel *et al.* (2012).

Table A2.2: List of the 15 functional traits measured for rainforest trees from French Guiana.

Functional trait	Unit	Nature	Ecological meaning	References
Laminar thickness	Mm	Continuous	Resource capture and defense	Niinemets (1999)
Laminar toughness	N	Continuous	Resource capture and defense	Agrawal & Fishbein (2006) Onoda <i>et al.</i> (2011)
Leaf tissue density	g cm ⁻³	Continuous	Resource capture and defense	Niinemets (1999) Kitajima & Poorter (2010)
Specific leaf area	m ² kg ⁻¹	Continuous	Resource capture and defense	Reich <i>et al.</i> (1997) Wright <i>et al.</i> (2004)
Leaf area	cm ²	Continuous	Resource capture	Wright <i>et al.</i> (2007)
Foliar carbon	cg g ⁻¹	Continuous	Resource capture and defense	Chaturvedi <i>et al.</i> (2011)
Foliar nitrogen	cg g ⁻¹	Continuous	Resource capture	Reich <i>et al.</i> (1997)
Foliar phosphorus	μg g ⁻¹	Continuous	Resource capture	Chaturvedi <i>et al.</i> (2011)
Foliar potassium	μg g ⁻¹	Continuous	Resource capture	Wright <i>et al.</i> (2005)
Foliar C : N ratio	cg g ⁻¹	Continuous	Resource capture and defense	Agrawal & Fishbein (2006)
Foliar ¹³C composition	‰	Continuous	Resource capture	Farquhar <i>et al.</i> (1989)
Laminar total chlorophyll	μg mm ⁻²	Continuous	Resource capture	Chaturvedi <i>et al.</i> (2011)
Trunk bark thickness	Mm	Continuous	Transport, structure, defense	Paine <i>et al.</i> (2010) Brando <i>et al.</i> (2012)
Stem wood specific gravity	N/A	Continuous	Transport, structure, defense	Chave <i>et al.</i> (2009)
Root wood specific gravity	N/A	Continuous	Transport, structure, defense	Chave <i>et al.</i> (2009)

Birds

To assess the functional structure of bird assemblages, seven traits describing aspects of the species life history and behavior (Table A2.3) were obtained for 86 species. Full description of trait measurements is found in Williams *et al.* (2010), a data paper that compiled distributional and functional trait information for vertebrates from the Australian Wet Tropics (AWT).

Table A2.3: List of the seven functional traits (life history and behavior) assessed for birds from the Australian Wet Tropics (AWT).

Functional trait	Calculation/ Class	Unit	Nature
Body mass	Average log-transformed body mass of adult individuals	g	Continuous
Clutch size	Average number of offspring produced in a single reproductive event	Number of individuals	Continuous
Reproductive seasonality	Seasonality of reproductive events: highly seasonal = all births \leq 2 months moderately seasonal = all births \leq 6 months aseasonal = births occurring over $>$ 6 months	N/A	Ordinal
Diet	Broad dietary preferences: A = seeds B = nectar or fruit with invertebrates C = $>$ 50 % invertebrates or vertebrates	N/A	Nominal
Activity period	Primary time of activity: A = diurnal B = nocturnal C = crepuscular	N/A	Nominal
Shelter type	Primary type of shelter recorded: protected = constructed nest, tree hollow intermediate = tree canopy, hollow log, nest on ground open = under shrubs, in grass	N/A	Nominal
Strata used	Primary type of strata of habitat used: A = terrestrial B = volant C = arboreal/terrestrial	N/A	Nominal

Appendix S3. Sensitivity analysis

The selected dimensions (Principal Coordinate axes – PcoA) to represent the functional space of each taxonomic group were composed by the first four, nine, and five PCoA axes for fishes, trees and birds, respectively (see criterion for this selection in Methods). To estimate if the selected number of dimensions has influenced the further results, we conducted a sensitivity analysis by adding or removing one axis at a time to build the functional spaces (e.g. for the fish dataset, besides the first four PCoA axes, we considered the first three and the first five axes). For each dataset (395 fishes, 262 trees, 86 birds) we firstly ordered the species from the rarest to the commonest (according to the Rarity Index) and divided into 10 classes of commonness, each containing 10% of the total number of species. We then computed the functional structure indices for each class. This procedure was conducted for each of the three treatments (i.e. number of dimensions used in the study +/- one). Finally, using the functional indices values for each commonness class, we calculated Person correlations between the original number of dimensions (i.e. used in the study) and the alternative numbers (i.e. +/- one PCoA axis).

For the three taxonomic groups, we found that the alternative treatments are highly correlated with the original number of dimensions, indicating that adding or removing one axis to compute the functional spaces should not affect the further results of this study (Figs. A3.1 – A3.3).

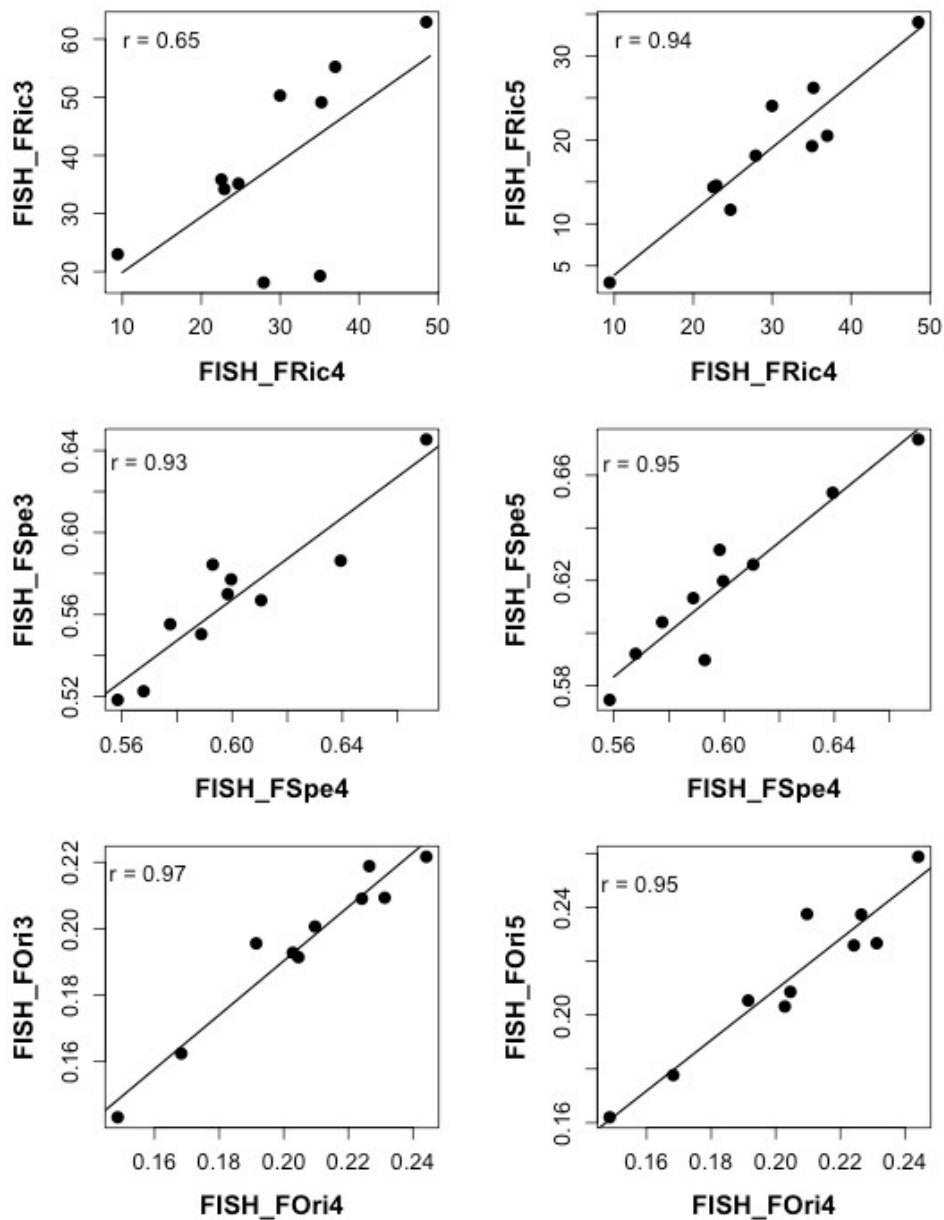


Figure A3.1 Correlation between functional indices (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOr) supported by each commonness class when the fish functional space was built with four (abscissas), three (ordinates in left figures), and five (ordinates in right figures) dimensions. Commonness classes contain 10% of the global pool of species (395 stream fishes from the Brazilian Amazon) and are ordered from the rarest to the commonest species.

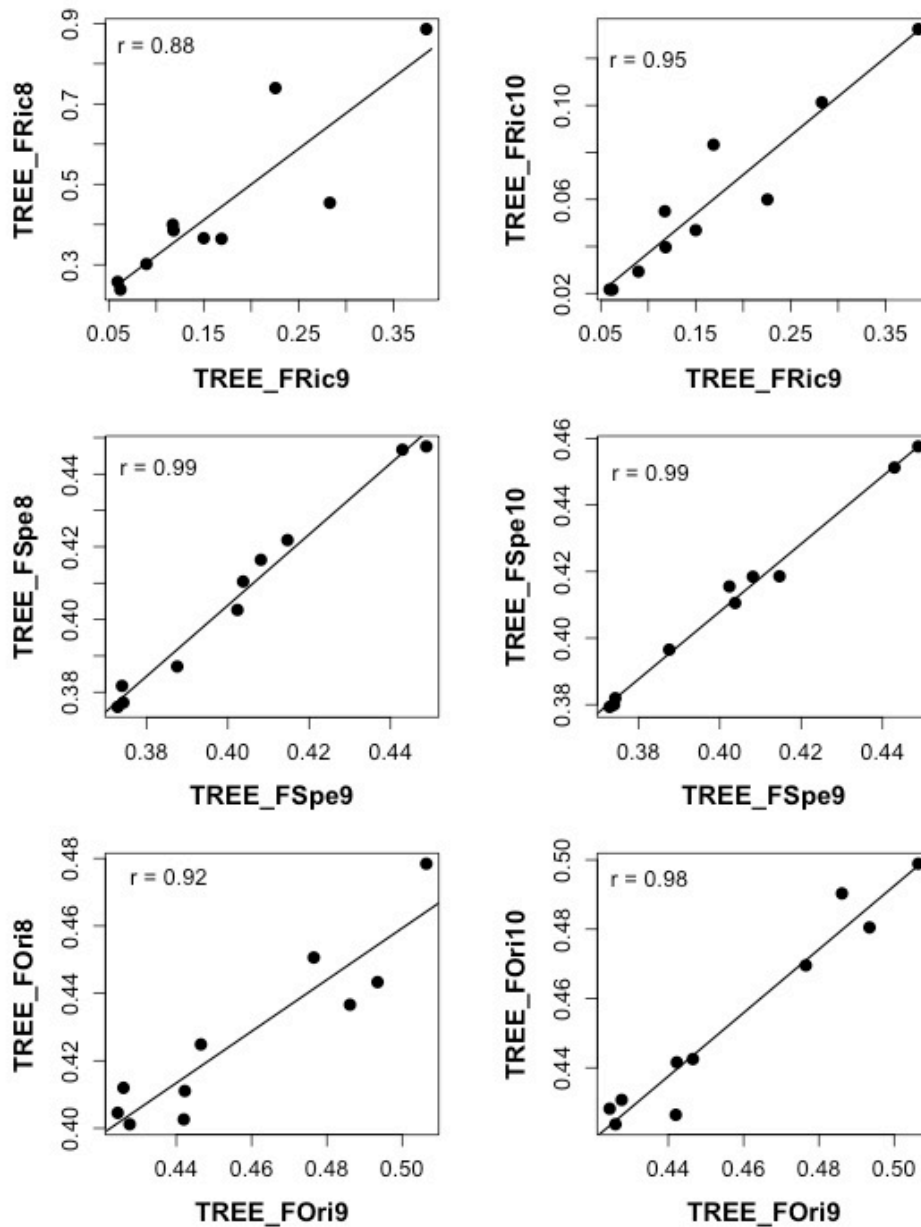


Figure A3.2 Correlation between functional indices (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOri) supported by each commonness class when the tree functional space was built with nine (abscissas), eight (ordinates in left figures), and ten (ordinates in right figures) dimensions. Commonness classes contain 10% of the global pool of species (262 rainforest trees from French Guiana) and are ordered from the rarest to the commonest species.

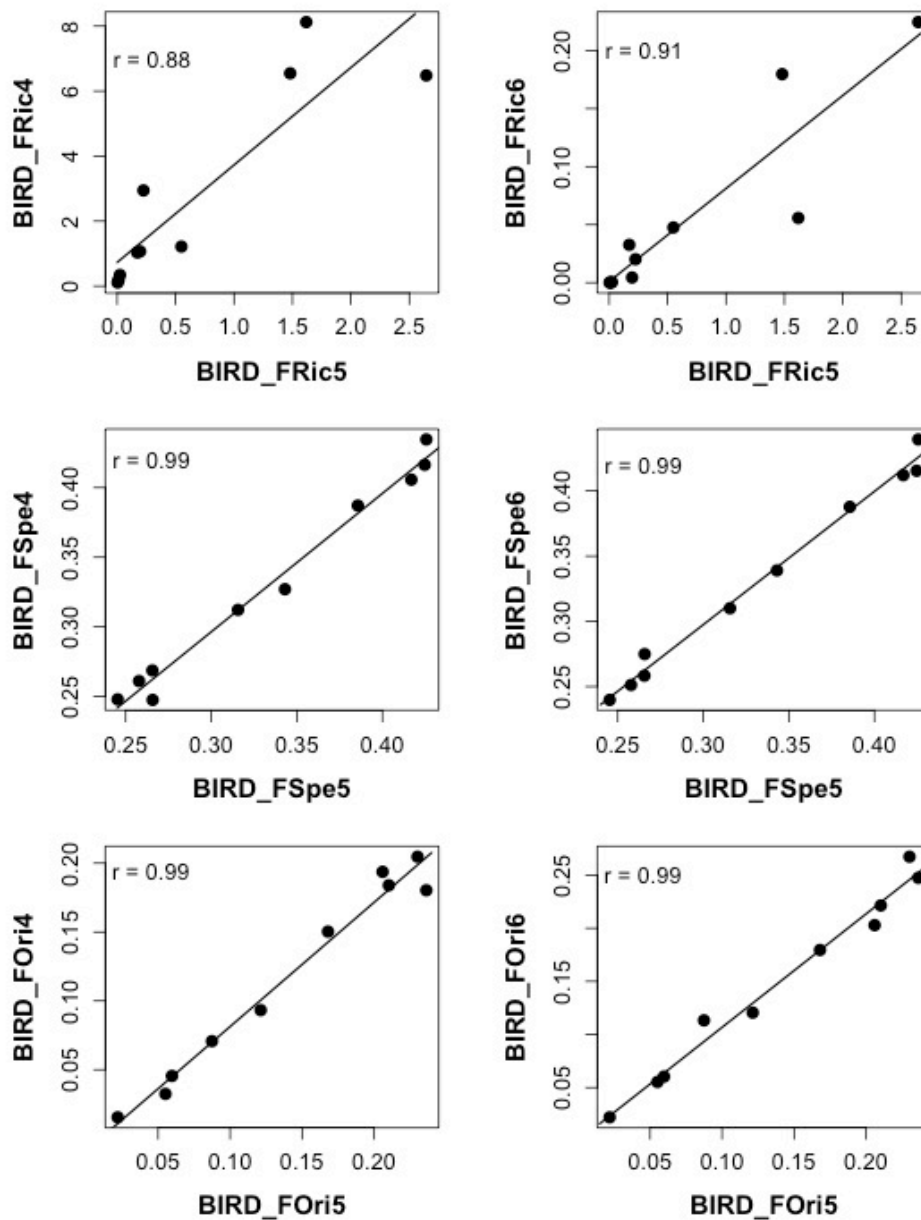


Figure A3.3 Correlation between functional indices (functional richness – FRic (%), mean specialization – FSpe, and mean originality – FOr) supported by each commonness class when the bird functional space was built with five (abscissas), four (ordinates in left figures), and six (ordinates in right figures) dimensions. Commonness classes contain 10% of the global pool of species (86 birds from the Australian Wet Tropics) and are ordered from the rarest to the commonest species.

SUPPLEMENTARY TABLES

Table S1: Friedman paired test (χ^2 ; p-value) comparing the functional structure – FS (functional richness – FRic, specialization – FSpe, and originality – FOr) of local assemblages (stream fishes from the Amazon, rainforest trees from French Guiana, and birds from Australian Wet Tropics) after species-loss simulations (from 10 to 90% of local richness) on three different scenarios: lose rarest species first; lose commonest species first; and lose species randomly (sampled in each local pool 1,000 times). N: number of local assemblages used for each level of species loss.

index	Species loss (%)	FISH			TREE			BIRD		
		χ^2	p	N	χ^2	p	N	χ^2	p	N
FRic	10	54.8	< 0.001	294	2.3	0.311	6	94.0	< 0.001	47
	20	80.3	< 0.001	294	4.0	0.135	6	94.0	< 0.001	47
	30	64.1	< 0.001	264	7.0	0.030	6	94.0	< 0.001	47
	40	79.3	< 0.001	246	12.0	0.002	6	94.0	< 0.001	47
	50	86.3	< 0.001	218	10.3	0.006	6	94.0	< 0.001	47
	60	104.6	< 0.001	149	12.0	0.002	6	94.0	< 0.001	47
	70	92.6	< 0.001	104	7.0	0.030	6	94.0	< 0.001	47
	80	48.2	< 0.001	39	1.5	0.472	4	94.0	< 0.001	47
	90	6.0	0.049	4	-	-	1	94.0	< 0.001	47
FSpe	10	49.4	< 0.001	319	1.0	0.607	6	94.0	< 0.001	47
	20	79.5	< 0.001	319	2.3	0.311	6	94.0	< 0.001	47
	30	66.9	< 0.001	319	9.3	0.009	6	94.0	< 0.001	47
	40	57.0	< 0.001	319	12.0	0.002	6	94.0	< 0.001	47
	50	67.2	< 0.001	319	12.0	0.002	6	94.0	< 0.001	47
	60	60.8	< 0.001	319	12.0	0.002	6	94.0	< 0.001	47
	70	63.8	< 0.001	319	10.3	0.006	6	94.0	< 0.001	47
	80	79.5	< 0.001	319	2.3	0.310	6	94.0	< 0.001	47
	90	49.5	< 0.001	319	1.0	0.607	6	94.0	< 0.001	47
FOr	10	110.2	< 0.001	319	1.3	0.513	6	94.0	< 0.001	47
	20	99.7	< 0.001	319	4.3	0.115	6	94.0	< 0.001	47
	30	40.4	< 0.001	319	10.3	0.006	6	94.0	< 0.001	47
	40	15.7	< 0.001	319	7.0	0.030	6	94.0	< 0.001	47
	50	3.3	0.193	319	10.3	0.006	6	94.0	< 0.001	47
	60	16.0	< 0.001	319	7.0	0.030	6	94.0	< 0.001	47
	70	42.7	< 0.001	319	8.3	0.016	6	94.0	< 0.001	47
	80	103.8	< 0.001	319	4.3	0.115	6	94.0	< 0.001	47
	90	116.7	< 0.001	319	1.3	0.513	6	94.0	< 0.001	47

Table S2: List of functions and R-packages for computations.

Main goal	Specific action	Function	Library
Rarity index	Geographic range (Extend of Occurrence – EOO)	SpatialPoints projection spTransform gArea	sp raster rgdal rgeos
Rarity index	Geographic distance	spDists	sp
Rarity index	Habitat breadth (Outlying Mean Index – OMI)	niche	ade4
Rarity index	Correlations among environmental factors Correlations among rarity facets	cor	stats
Functional structure	Dissimilarity matrix (Gower or Euclidean distance)	daisy	cluster
Functional structure	Synthetic axes for multidimensional functional space	pcoa	ape
Functional structure	Quality of functional space	mantel	vegan
Functional structure	Functional richness – FRic	convhulln	geometry
Functional structure	Functional specialization – FSpe Functional originality – FOri	* adapted from FDind FDchange	ape geometry
Data analysis	Ordinary least square regressions	lm	stats
Data analysis	Randomizations for null models	sample	base

* <http://www.ecosym.univ-montp2.fr/software>

SUPPLEMENTARY FIGURES

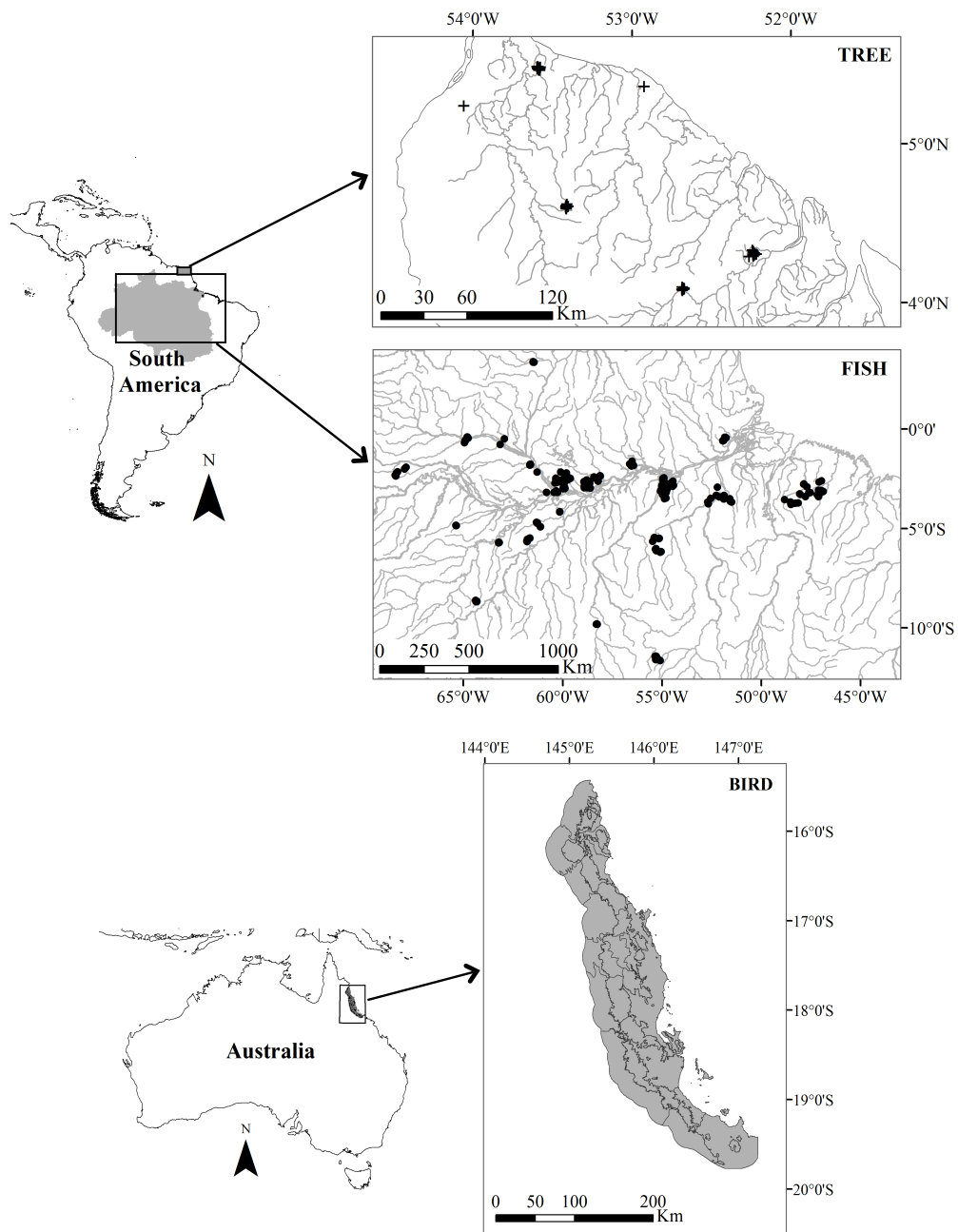


Figure S1: Geographic locations sampled for rainforest trees from French Guiana (36 plots represented by black cross), stream fishes from the Brazilian Amazon (320 sites represented by black dots; gray polygon in South America map delimiting the Brazilian Amazon Basin), and birds from the Australian Wet Tropics (47 subregions).

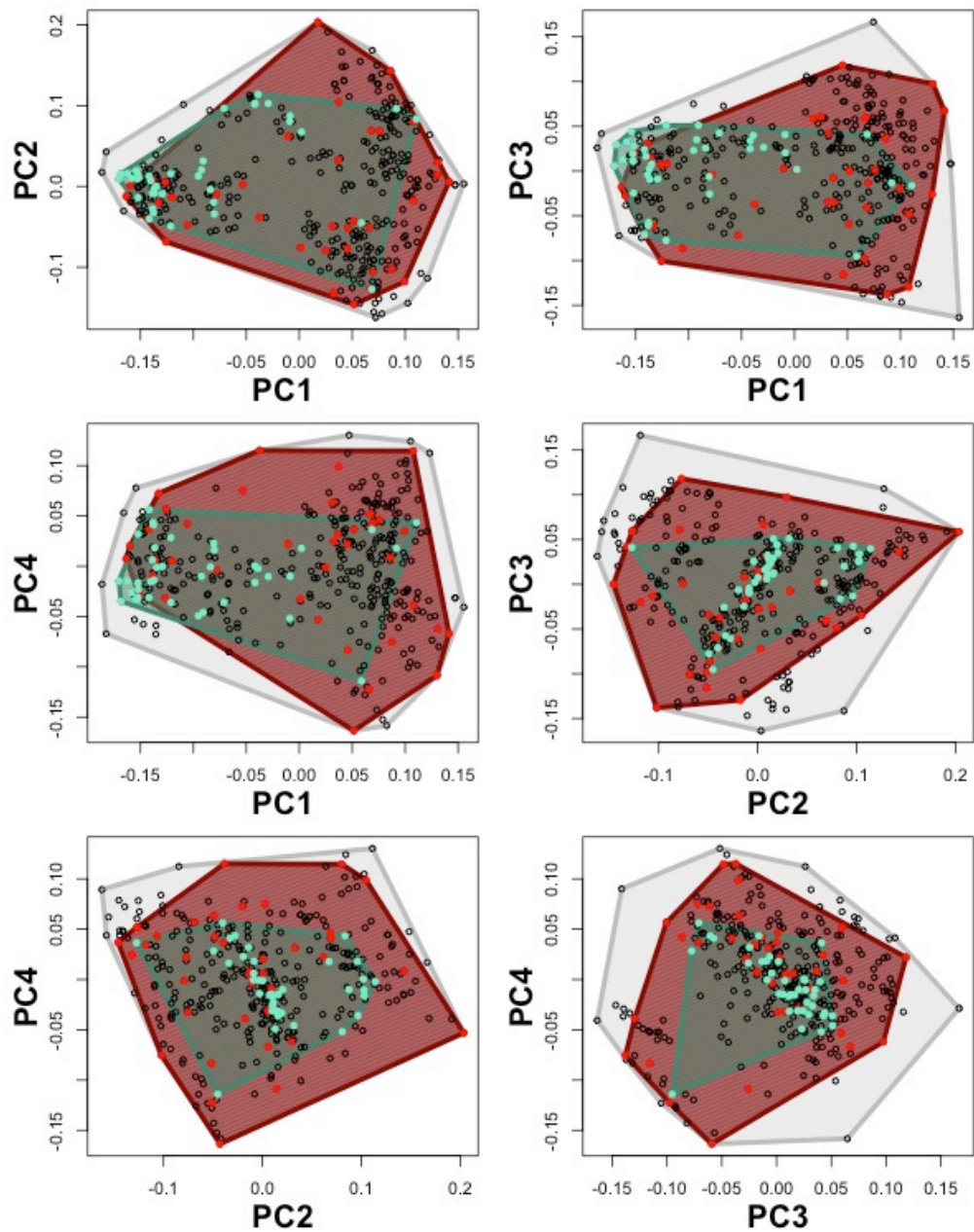


Figure S2: Four-dimensional functional space of the regional pool of stream fishes from the Amazon (395 species). Each plot represents two axes of a Principal Coordinate Analysis (PC), where species are plotted with circles according to their respective trait values. The 10% rarest and 10% commonest species are filled with red and green, respectively. Projections of the convex hull volumes are illustrated by the polygons embedding: all species (gray), the 10% rarest (red), and the 10% commonest (green) species.

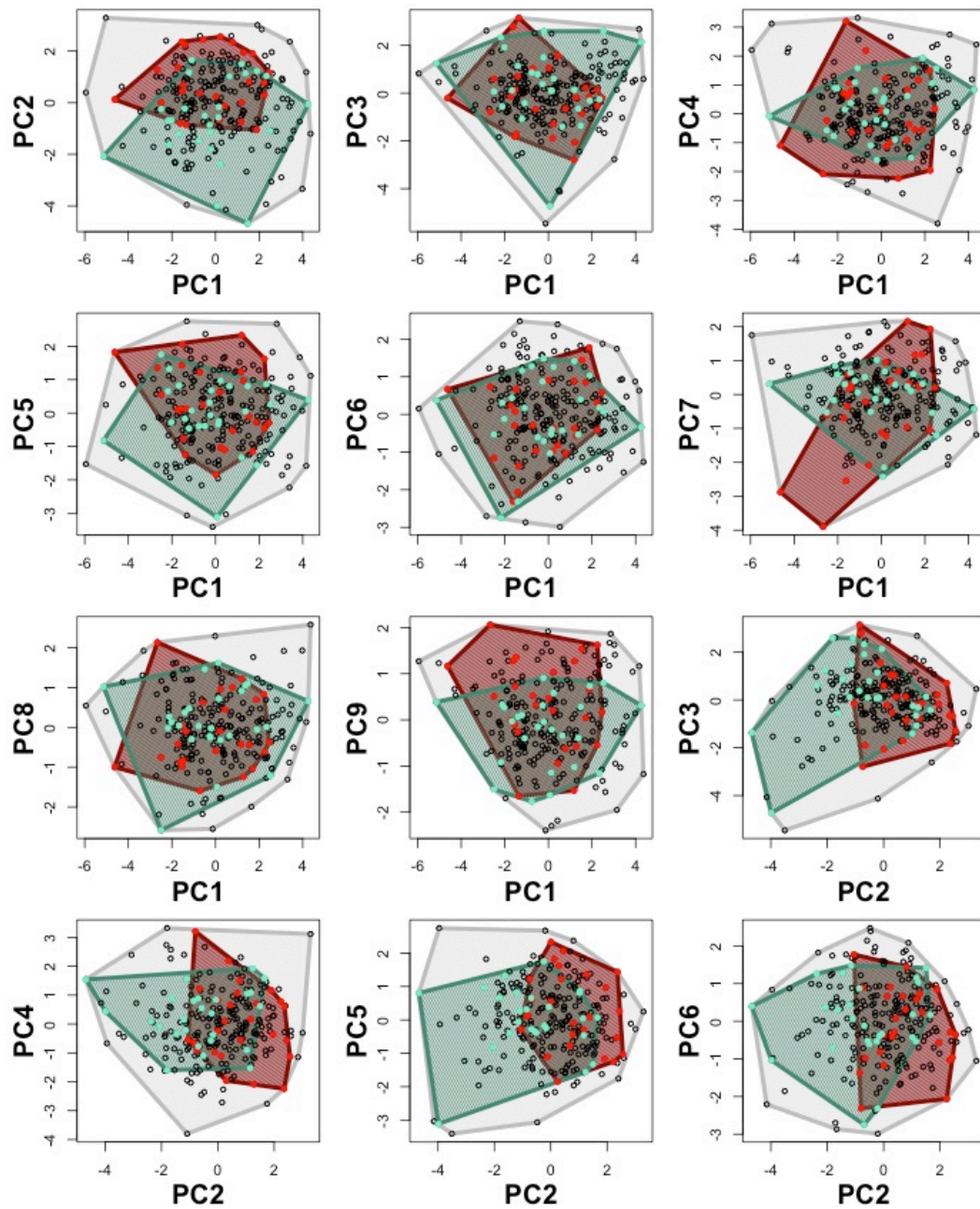


Figure S3: Nine-dimensional functional space of the regional pool of rainforest trees from French Guiana (262 species). Each plot represents two axes of a Principal Coordinate Analysis (PC), where species are plotted with circles according to their respective trait values. The 10% rarest and 10% commonest species are filled with red and green, respectively. Projections of the convex hull volumes are illustrated by the polygons embedding: all species (gray), the 10% rarest (red), and the 10% commonest (green) species.

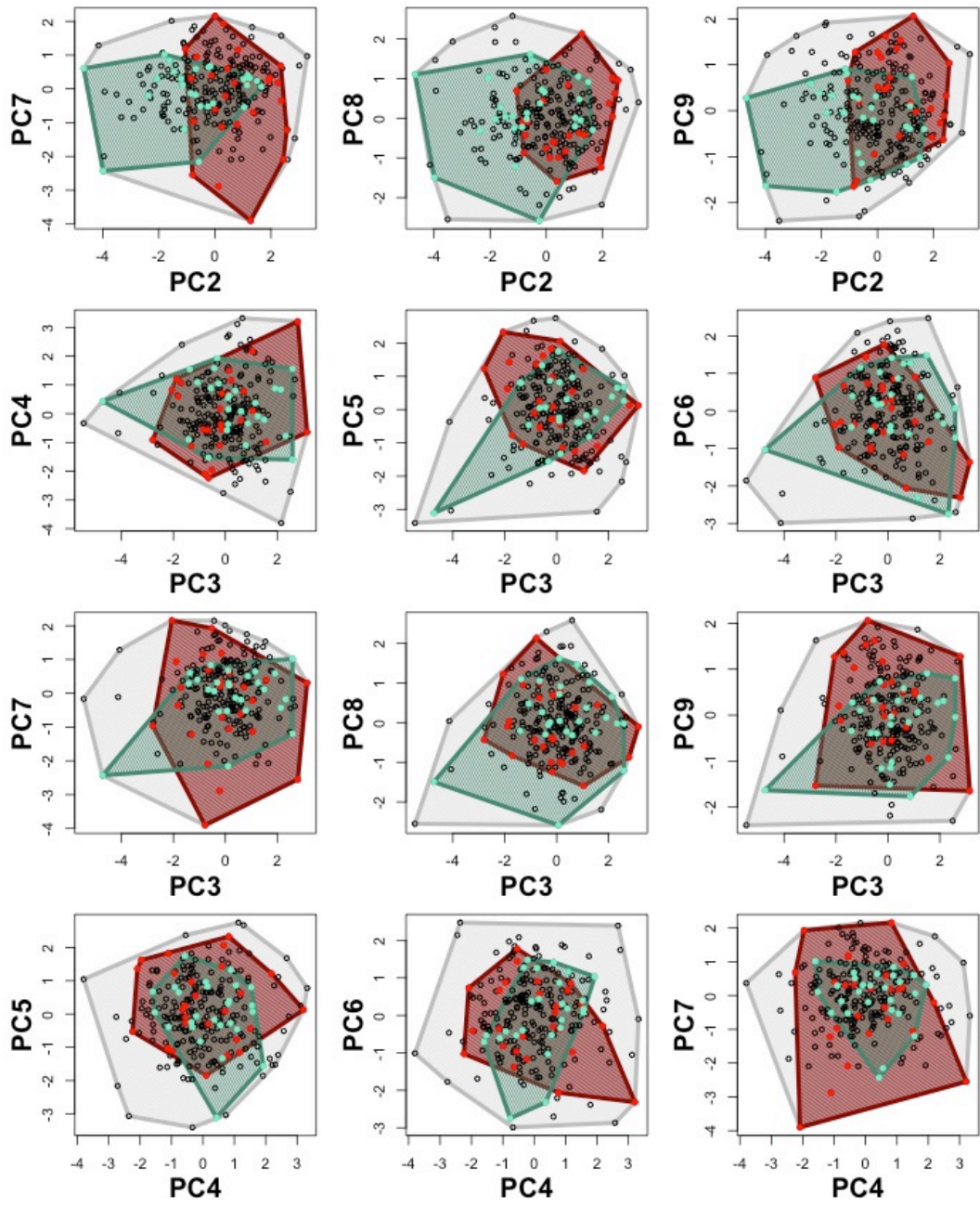


Figure S3 (continuation)

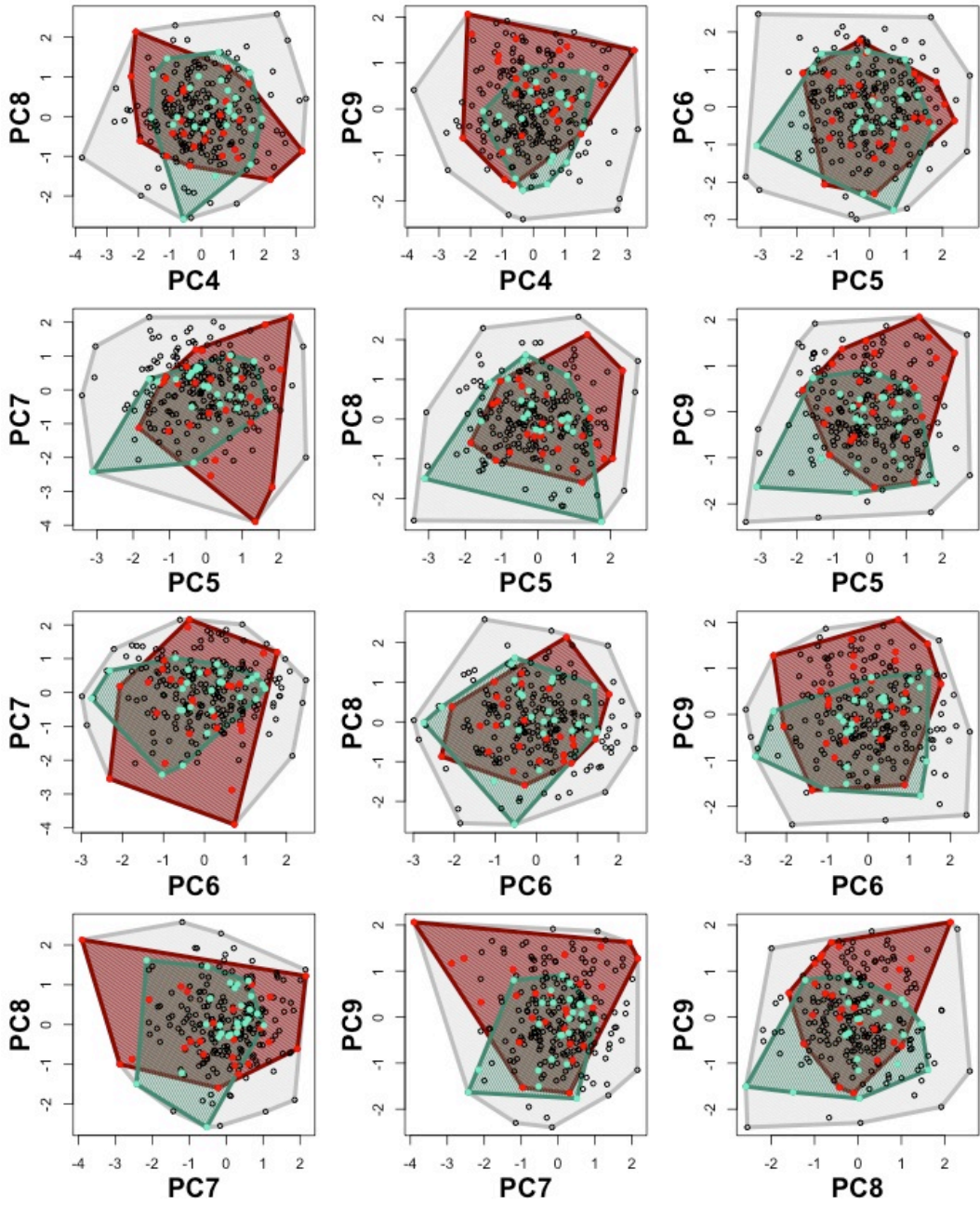


Figure S3 (continuation)

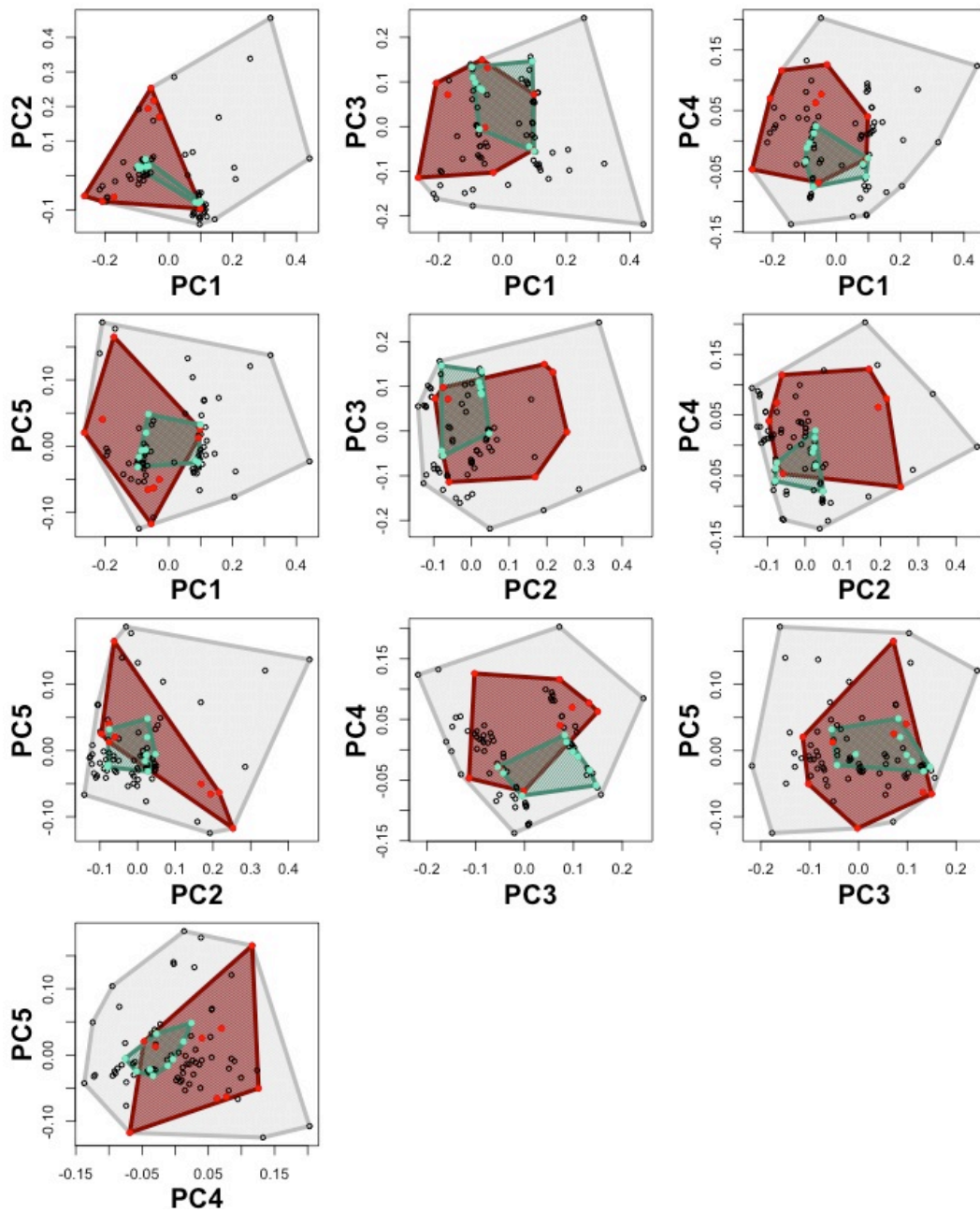


Figure S4: Five-dimensional functional space of the regional pool of birds from the Australian Wet Tropics (86 species). Each plot represents two axes of a Principal Coordinate Analysis (PC), where species are plotted with circles according to their respective trait values. The 10% rarest and 10% commonest species are filled with red and green, respectively. Projections of the convex hull volumes are illustrated by the polygons embedding: all species (gray), the 10% rarest (red), and the 10% commonest (green) species.

SUPPLEMENTARY REFERENCES

- Agrawal, A.A. & Fishbein, M. (2006) Plant defense syndromes. *Ecology*, **87**, S132–S149.
- Baraloto, C., Paine, C.E.T., Patino, S., Bonal, D., Hérault, B. & Chave, J. (2010a) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, **24**, 208–216.
- Baraloto, C., Paine, C.E.T., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.M., Hérault, B., Patiño, S., Roggy, J.C. & Chave, J. (2010b) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338–1347.
- Baraloto, C., Molto, Q., Rabaud, S., Hérault, B., Valencia, R., Blanc, L., Fine, P.V.A. & Thompson, J. (2013) Rapid simultaneous estimation of aboveground biomass and tree diversity across Neotropical forests: a comparison of field inventory methods. *Biotropica*, **45**, 288–298.
- Boyle, K.S. & Horn, M.H. (2006) Comparison of feeding guild structure and ecomorphology of intertidal fish assemblages from central California and central Chile. *Marine Ecology Progress Series*, **319**, 65–84.
- Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. & Putz, F.E. (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.
- Chaturvedi, R.K., Raghubanshi, A.S. & Singh, J.S. (2011) Leaf attributes and tree growth in a tropical dry forest. *Journal of Vegetation Science*, **22**, 917–931.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Dumay, O., Tari, P.S., Tomasini, J.A. & Mouillot, D. (2004) Functional groups of lagoon fish species in Languedoc Roussillon, southern France. *Journal of Fish Biology*, **64**, 970–983.

- Farquhar, G.D., Ehleringer, J.R. & Hubick, K.T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 503–537.
- Fortunel, C., Fine, P.V.A. & Baraloto, C. (2012) Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology*, **26**, 1153–1161.
- Fortunel, C., Paine, C.E.T., Fine, P.V.A., Kraft, N.J.B. & Baraloto, C. (2014) Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology*, **102**, 145–155.
- Fulton, C.J., Bellwood, D.R. & Wainwright, P.C. (2001) The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology*, **139**, 25–33.
- Gatz, A.J. (1979) Community organization in fishes as indicated by morphological features. *Ecology*, **60**, 711–718.
- Karpouzi, V.S. & Stergiou, K.I. (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology*, **62**, 1353–1365.
- Keenleyside, M.H.A. (1979) *Diversity and adaptation in fish behaviour*. Springer-Verlag, Berlin.
- Kitajima, K. & Poorter, L. (2010) Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist*, **186**, 708–721.
- Mendonça, F.P., Magnusson, W.E. & Zuanon, J. (2005) Relationships between habitat characteristics and fish assemblages in small streams of Central Amazonia. *Copeia*, **2005**, 750–763.

Niinemets, U. (1999) Components of leaf dry mass per area – thickness and density – alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist*, **144**, 35–47.

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C., Díaz, S., Dominy, N.J., Elgart, A., Enrico, L., Fine, P.V., Howard, J.J., Jalili, A., Kitajima, K., Kurokawa, H., McArthur, C., Lucas, P.W., Markesteijn, L., Pérez-Harguindeguy, N., Poorter, L., Richards, L., Santiago, L.S., Sosinski Jr, E.E., Van Bael, S.A., Warton, D.I., Wright, I.J., Wright, S.J. & Yamashita, N. (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, **14**, 301–312.

Paine, C.E.T., Stahl, C., Courtois, E.A., Patino, S., Sarmiento, C. & Baraloto, C. (2010) Functional explanations for variation in bark thickness in tropical rain forest trees. *Functional Ecology*, **24**, 1202–1210.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA*, **94**, 13730–13734.

Sazima, I. (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology*, **29**, 53–65.

Sibbing, F.A., & Nagelkerke, L.A.J. (2001). Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries*, **10**, 393–437.

Villéger, S., Miranda, J.R., Hernandez, D.F. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, **20**, 1512–1522.

Webb, P.W. (1984) Form and function in fish swimming. *Scientific American*, **251**, 72–82.

Williams, S.E., VanDerWal, J., Isaac, J., Shoo, L.P., Storlie, C., Fox, S., Bolitho, E.E., Moritz, C., Hoskin, C.J. & Williams, Y.M. (2010) Distributions, life-history specialization,

and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology*, **91**, 2493.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M. Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I., & Westoby, M. (2005) Assessing the generality of global leaf trait relationships. *New Phytologist*, **166**, 485–496.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Paz, H., Pitman, N.C.A., Poorter, L., Silman, M.R., Vriesendorp, C.F., Webb, C.O., Westoby, M & Wright, S.J. (2007) Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany*, **99**, 1003–1015.

SYNTHESIS

The application of trait-based approaches in community ecology is becoming more frequent and is proving to be a powerful tool to handle with both theoretical (e.g., assembly rules) and applied issues (McGill *et al.* 2006; Mouillot *et al.* 2013b). Given the scarcity of conservation resources and the subsequent problem of triage (i.e., the most reasonable choice within the trade-off economic-conservation values; Cadotte & Davies 2010), providing the most complete possible understanding of the biotic responses to the increasing levels of human-induced impacts is critical. In a second step, more than just disentangling the current multiple effects of environmental changes on biodiversity, we also need to predict the consequences of species extinction to the structure of communities and to the ecological processes within ecosystems. Under a utilitarian view of biodiversity, losing ecosystem functioning means imperil the provisioning of ecosystem goods and services (Naeem *et al.* 2012). In this context, assessing the multiple facets of assemblage functional structure seems a very appropriate strategy since the diversity of ecological processes is likely closely related to the diversity of species functional traits (i.e., species with different traits perform complementary roles; Díaz & Cabido 2001; Hooper *et al.* 2005; Mouillot *et al.* 2011).

Surprisingly, the functional structure of assemblages was scarcely linked with conservation issues, especially in tropical ecosystems, which support enormous diversity of species and currently suffer dramatic landscape changes (Hansen *et al.* 2008; Peres *et al.* 2010; Gardner *et al.* 2013). Here, we tried to make this link for stream fish assemblages in the Brazilian Amazon by assessing species traits in the context of two central questions in conservation biology: 1) How do landscape changes affect species assemblages and potentially alter ecological processes and the functioning of ecosystems? 2) Do rare species, which are more vulnerable to go extinct, play important and original roles within assemblages or they only add redundant functions to tropical systems?

We found that multiple drivers operating at different spatial scales and pathways influence the functional structure of the fish assemblages. For instance, removing local riparian forests results in increased coverage of submerged vegetation in streams. This instream alteration led to domination of a few trait combinations (i.e., under this habitat condition the most abundant species tend to be functionally similar). This may have critical consequences if aggregate

community properties are important to ecological processes such as resistance to invasive species introductions. Moreover, deforestation alters the channel morphology and the bed stability and complexity of streams, changing the assemblage functional identity (e.g., due to the disproportionate negative effects on traits associated with the use of the benthic compartment). One of the most remarkable findings of our investigation is the strong negative effect of riverscape fragmentation (i.e., density of roads crossing the streams) on several facets of the functional diversity and structure of the fish assemblages. Specifically, our results indicate that losing regional connectivity potentially reduces the range of niche occupation and tends to functionally homogenize local assemblages. These results are likely linked to dispersal constraints for species unable to establish stable local populations in small streams such as the large carnivorous (i.e., a key functional entity in the functioning of streams; Jackson *et al.* 2001). Therefore, more than the purely assessment of land cover (i.e., % deforestation), it is imperative to take into account the levels of fragmentation across riverscapes. This is definitely a critical concern for the mid-eastern Amazon, where the rapid agricultural development is resulting in highly fragmented landscapes.

The effects of losing hydrological connectivity on the functional structure of these fish assemblages align with metacommunity paradigms (*sensu* Leibold *et al.* 2004), particularly when considering source-sink dynamics between large rivers and small tributaries, or species-sorting effects (e.g. dispersal allowing compositional changes across different headwaters). An increasing body of literature is applying such concepts to understand the relative role of local vs. regional scale effects of anthropogenic disturbances on freshwater assemblages (e.g., Falke & Fausch 2010, Johnson *et al.* 2013), but linking metacommunity with functional perspectives is still incipient (Erös *et al.* 2012). We believe this is a promising research field in the assessment of fragmentation consequences in Amazonian streams. Keeping the respective proportions, such perspectives should also be scaled to the Amazonian large rivers, which harbor innumerable species of commercial interest and are being strongly fragmented by colossal impoundments.

The first part of this thesis is a comprehensive multi-scale assessment of the condition of headwater streams and their ichthyofauna in two highly human-modified regions of the Amazon. We believe that the results therein underscore the importance of some landscape changes often unrecognized, such as road crossings and agriculture intensification that can have a marked effect on these ecosystems. Drawing on the relationships observed in our data

we expect that this investigation provide useful insights to suggest priorities for the improved management of stream biodiversity. Nevertheless, we also recognize that it is only a starting point and we still need much effort to fill important gaps (e.g., basic knowledge of the species natural history) to achieve a satisfactory understanding of the relationship between landscape changes and the Amazonian stream biota. Finally, although its unequivocal value to produce predictive models of land-use effects on species assemblages and ecosystems, this kind of assessment does not provide tools to forecast the functional consequences of species extinctions.

Trying to achieve this latter goal, in the second part of the thesis we designed scenarios of species loss using a dataset that comprises fish sampling across hundreds of well-preserved streams in the Amazon Basin (i.e., potentially representing the natural structure of the assemblages). Given that rare species are likely the first to go extinct under ever-increasing human-induced disturbances, we tested their contribution to the functional structure of species assemblages using realistic simulations. To enhance the generality of our findings, we applied the same framework to other two sets of species-rich tropical assemblages: trees from French Guiana, and birds from the Australian Wet Tropics.

All our scenarios of species loss demonstrate a disproportionate impact of rare species extinction on the functional structure of the assemblages compared to a random loss, both at local and regional scales. In other words, losing rare species would reduce the functional diversity of assemblages more than expected under a random loss of species. The generality of these findings is strengthened by the similar patterns observed among three taxonomic groups highly distinct in terms of evolutionary history. These results potentially have deep implications for tropical conservation. They justify the application of the precautionary principle for tropical biodiversity conservation, despite the expected buffering effects provided by functional redundancy in such species-rich systems.

REFERENCES

- Agrawal, A.A.; Fishbein, M. 2006. Plant defense syndromes. *Ecology*, 87: S132-S149.
- Allan, J.D.; Erickson, D.L.; Fay, F. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology*, 37: 149-161.
- Allan, J.D. 2004. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 35: 257-284.
- Baltz, D.M.; Moyle, P.B. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications*, 3: 246-255.
- Baraloto, C.; Paine, C.E.T.; Patino, S.; Bonal, D.; Hérault, B.; Chave, J. 2010a. Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, 24: 208-216.
- Baraloto, C.; Paine, C.E.T.; Poorter, L.; Beauchene, J.; Bonal, D.; Domenach, A.M.; Hérault, B.; Patiño, S.; Roggy, J.C.; Chave, J. 2010b. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, 13: 1338-1347.
- Baraloto, C.; Rabaud, S.; Molto, Q.; Blanc, L.; Fortunel, C.; Hérault, B.; Dávila, N.; Mesones, I.; Rios, M.; Valderrama, E.; Fine, P.V.A. 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, 17: 2677-2688.
- Baraloto, C.; Molto, Q.; Rabaud, S.; Hérault, B.; Valencia, R.; Blanc, L.; Fine, P.V.A.; Thompson, J. 2013. Rapid simultaneous estimation of aboveground biomass and tree diversity across Neotropical forests: a comparison of field inventory methods. *Biotropica*, 45: 288-298.
- Barnosky, A.D.; Matzke, N.; Tomiya, S.; Wogan, G.O.U.; Swartz, B.; Quental, T.B.; Marshall, C.; McGuire, J.L.; Lindsey, E.L.; Maguire, K.C.; Mersey, B.; Ferrer, E.A. 2011.

Has the Earth's sixth mass extinction already arrived? *Nature*, 471: 51-57.

Bellwood, D.R.; Wainwright, P.C.; Fulton, C.J.; Hoey, A.S. 2006. Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B*, 273: 101-107.

Bermann, C. 2002. *Energia no Brasil: para quê? Para quem? Crise e alternativas para um país sustentável*. 2da ed. Livraria da Física, São Paulo, 139p.

Bojsen, B.H.; Barriga, R. 2002. Effects of deforestation on fish community structure in Ecuadorian Amazon streams. *Freshwater Biology*, 47: 2246-2260.

Bollen, K.A.; Stine, R.A. 1992. Bootstrapping goodness-of-fit measures in structural equation models. *Sociological Methods and Research*, 21: 205-229.

Boyle, K.S.; Horn, M.H. 2006. Comparison of feeding guild structure and ecomorphology of intertidal fish assemblages from central California and central Chile. *Marine Ecology Progress Series*, 319: 65-84.

Bracken, M.E.S.; Low, N.H.N. 2012. Realistic losses of rare species disproportionately impact higher trophic levels. *Ecology Letters*, 15: 461-467.

Brando, P.M.; Nepstad, D.C.; Balch, J.K.; Bolker, B.; Christman, M.C.; Coe, M.; Putz, F.E.; 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, 18: 630-641.

Brook, B.W.; Bradshaw, C.J.A.; Koh, L.P.; Sodhi, N.S. 2006. Momentum drives in the crash: mass extinction in the tropics. *Biotropica*, 38: 302-305.

Brooks, T.M.; Mittermeier, R.A.; Fonseca, G.A.B.; Gerlach, J.; Hoffmann, M.; Lamoreux, J.F.; Mittermeier, C.G.; Pilgrim, J.D.; Rodrigues, A.S.L. 2006. Global biodiversity conservation priorities. *Science*, 313: 58-61.

Bryce, S.A.; Lomnický, G.A.; Kaufmann, P.R. 2010. Protecting sediment-sensitive aquatic species in mountain streams through the application of biologically based sediment criteria. *Journal of the North American Benthological Society*, 29: 657-672.

- Bush, M.B. 1994. Amazonian speciation: a necessarily complex model. *Journal of Biogeography*, 21: 5-17.
- Bush, M.B.; Silman, M.R. 2007. Amazonian exploitation revisited: ecological asymmetry and the policy pendulum. *Frontiers in Ecology and the Environment*, 5: 457-465.
- Cadotte, M.W.; Davies, T.J. 2010. Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, 16: 376-385.
- Cadotte, M.W.; Davies, T.J.; Regetz, J.; Kembel, S.W.; Cleland, E.E.; Oakley, T.H. 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters*, 13: 96-105.
- Carvalho, L.N.; Zuanon, J.; Sazima, I. 2006. The almost invisible league: crypsis and association between minute fishes and shrimps as a possible defence against visually hunting predators. *Neotropical Ichthyology*, 4(2): 219-224.
- Carvalho, L.N.; Zuanon, J.; Sazima, I. 2009. Natural History of Amazon Fishes. In: Del Claro, K.; Oliveira, P.S.; Rico-Gray, V. (Eds.). *Tropical biology and conservation management: case studies*. Eolss Publishers Co. Ltd., Oxford, UK, p.113-144.
- Carvalho, M.S.; Zuanon, J.A.S.; Ferreira, E.J.G. 2014. Diving in the sand: the natural history of *Pygidianops amphioxus* (Siluriformes: Trichomycteridae), a miniature catfish of Central Amazonian streams in Brazil. *Environmental Biology of Fishes*, 97: 59-68.
- Casatti, L.; Langeani, F.; Silva, A.M.; Castro, R.M.C. 2006. Stream fish, water and habitat quality in a pasture dominated basin, southeastern Brazil. *Brazilian Journal of Biology*, 66: 681-696.
- Casatti, L.; Teresa, F.B.; Gonçalves-Souza, T.; Bessa, E.; Manzotti, A.R.; Gonçalves, C.S.; Zeni, J.O. 2012. From forests to cattail: how does the riparian zone influence stream fish? *Neotropical Ichthyology*, 10: 205-214.

Castello, L.; McGrath, D.G.; Hess, L.L.; Coe, M.T.; Lefebvre, P.A.; Petry, P.; Macedo, M.N.; Renó, V.F.; Arantes, C.C. 2013. The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, 6: 217-229.

Castro, R.M.C. 1999. Evolução da ictiofauna de riachos sul-americanos: padrões gerais e possíveis processos causais. In: Caramaschi, E.P.; Mazzoni, R.; Peres-Neto, P.R. (Eds.). *Ecologia de peixes de riachos. Série Oecologia Brasiliensis*. PPGE-UFRJ, Rio de Janeiro, Brasil, p.139-155.

Chapman, L. J.; Chapman, C.A. 2002. Tropical forest degradation and aquatic ecosystems: our current state of knowledge. In: Collares-Pereira, M.J.; Cowx, I.G.; Coelho, M.M. (Eds.). *Conservation of freshwater fishes: options for the future*. Blackwell Science, Oxford, UK, p.237-249.

Chaturvedi, R.K.; Raghubanshi, A.S.; Singh, J.S. 2011. Leaf attributes and tree growth in a tropical dry forest. *Journal of Vegetation Science*, 22: 917-931.

Chave, J.; Coomes, D.; Jansen, S.; Lewis, S.L.; Swenson, N.G.; Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters*, 12: 351-366.

Coddington, J.A.; Agnarsson I.; Miller, J.A.; Kuntner, M.; Hormiga, G. 2009. Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology*, 78: 573-584.

Colinvaux, P.A.; de Oliveira, P.E.; Bush, M.B. 2000. Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews*, 19: 141-169.

Condit, R.; Pitman, N.; Leigh Jr., E.G.; Chave, J.; Terborgh, J.; Foster, R.B.; Núñez, P.; Aguilar, S.; Valencia, R.; Villa, G.; Muller-Landau, H.C.; Losos, E.; Hubbell, S.P. 2002. Beta-diversity in tropical forest trees. *Science*, 295: 666-669.

Cornwell, W.K.; Schwilk, D.W.; Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87: 1465-1471.

Davies, K.F.; Margules, C.R.; Lawrence, J.F. 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology*, 85: 265-271.

Diáz, S.; Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16: 646-655.

Dolédec, S.; Chessel, D.; Gimaret-Carpentier, C. 2000. Niche separation in community analysis: a new method. *Ecology*, 81: 2914-2927.

Dumay, O. ; Tari, P.S. ; Tomasini, J.A. ; Mouillot, D. 2004. Functional groups of lagoon fish species in Languedoc Roussillon, southern France. *Journal of Fish Biology*, 64: 970-983.

Ernst, R.; Linsenmair, K.E.; Rodel, M.O. 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biological Conservation*, 133: 143-155.

Erős, T.; Sály, P.; Takács, P.; Specziár, A.; Bíró, P. 2012. Temporal variability in the spatial and environmental determinants of functional metacommunity organization – stream fish in a human-modified landscape. *Freshwater Biology*, 57: 1914-1928.

Espírito-Santo, H.M.V.; Magnusson, W.E.; Zuanon, J.; Mendonça, F.P.; Landeiro, V.L. 2009. Seasonal variation in the composition of fish assemblages in small Amazonian forest streams: evidence for predictable changes. *Freshwater Biology*, 54: 536-548.

Espírito-Santo, H.M.V.; Rodriguez, M.A.; Zuanon, J. 2013. Reproductive strategies of Amazonian stream fishes and their fine-scale use of habitat are ordered along a hydrological gradient. *Freshwater Biology*, 58: 2494-2504.

Falke, J.A.; Fausch, K.D. 2010. From metapopulations to metacommunities: linking theory with empirical observations of the spatial and population dynamics of stream fishes. In: Gido, K.B.; Jackson, D.A. (Eds.). *Community ecology of stream fishes: concepts, approaches, and*

techniques. American Fisheries Society, Maryland, USA, p.207-233.

FAO. 2011. *The State of Forests in the Amazon Basin, Congo Basin and Southeast Asia*. Food and Agriculture Organization of the United Nations, Rome, 80p.

Farquhar, G.D.; Ehleringer, J.R.; Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40: 503-537.

Fausch, K.D.; Torgersen, C.E.; Baxter, C.V.; Li, H.W. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience*, 52: 483-98.

Fearnside, P.M. 2006. Desmatamento na Amazônia: dinâmica, impactos e controle. *Acta Amazonica*, 36(3): 395-400.

Ferreira, J.; Aragão, L.E.O.C.; Barlow, J.; Barreto, P.; Berenguer, E.; Bustamante, M.; Gardner, T.A.; Lees, A.C.; Lima, A.; Louzada, J.; Pardini, R.; Parry, L.; Peres, C.A.; Pompeu, P.S.; Tbarelli, M.; Zuanon, J. 2014. Brazil's environmental leadership at risk: mining and dams threaten protected areas. *Science*, 346: 706-707.

Fey, S.B.; Siepielski, A.M.; Nusslé, S.; Cervantes-Yoshida, K.; Hwan, J.L.; Huber, E.R.; Fey, M.J.; Catenazzi, A.; Carlson, S.M. 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences USA*, 112: 1083-1088.

Flynn, D.F.B.; Gogol-Prokurat, M.; Nogeire, T.; Molinari, N.; Richers, B.T.; Lin, B.B.; Simpson, N.; Mayfield, M.M.; DeClerck, F. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, 12: 22-33.

Fortunel, C., Fine, P.V.A. & Baraloto, C. (2012) Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology*, **26**, 1153–1161.

Fortunel, C.; Paine, C.E.T.; Fine, P.V.A.; Kraft, N.J.B.; Baraloto, C. 2014. Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology*,

102: 145-155.

Frederico, R.G. 2014. *Explorando o nicho de peixes de água doce: uma abordagem evolutiva e conservacionista em igarapés de terra firme amazônicos*. Tese de Doutorado, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM. 123p.

Fulton, C.J.; Bellwood, D.R.; Wainwright, P.C. 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology*, 139: 25-33.

Gardner, T.A.; Barlow, J.; Parry, L.T.W.; Peres, C.A. 2007. Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica*, 39: 25-30.

Gardner, T.A.; Ferreira, J.; Barlow, J.; Lees, A.; Parry, L.; Vieira, I.C.G.; Berenguer, E.; Abramovay, R.; Aleixo, A.; Andretti, C.; Aragão, L.E.O.C.; Araújo, I.; Ávila, W.S.; Bardgett, R.D.; Batistella, M.; Begotti, R.A.; Beldini, T.; Blas, D.E.; Braga, R.F.; Braga, D.L.; Brito, J.G.; Camargo, P.B.; Santos, F.C.; Oliveira, V.C.; Cordeiro, A.C.N.; Cardoso, T.M.; Carvalho, D.R.; Castelani, S.A.; Chaul, J.C.M.; Cerri, C.E.; Costa, F.A.; Costa, C.D.F.; Coudel, E.; Coutinho, A.C.; Cunha, D.; D'Antona, A.; Dezincourt, J.; Dias-Silva, K.; Durigan, M.; Esquerdo, J.C.D.M.; Feres, J.; Ferraz, S.F.B.; Ferreira, A.E.M.; Fiorini, A.C.; Silva, L.V.F.; Frazão, F.S.; Garrett, R.; Gomes, A.S.; Gonçalves, K.S.; Guerrero, J.B.; Hamada, N.; Hughes, R.M.; Iglioni, D.C.; Jesus, E.C.; Juen, L.; Junior, M.; Junior, J.M.B.O.; Junior, R.C.O.; Junior, C.S.; Kaufmann, P.; Korasaki, V.; Leal, C.G.; Leitão, R.P.; Lima, N.; Almeida, M.F.L.; Lourival, R.; Louzada, J.; Nally, R.M.; Marchand, S.; Maués, M.M.; Moreira, F.M.S.; Morsello, C.; Moura, N.; Nessimian, J.; Nunes, S.; Oliveira, V.H.F.; Pardini, R.; Pereira, H.C.; Pompeu, P.S.; Ribas, C.R.; Rossetti, F.; Schmidt, F.A.; Siva, R.; Silva, R.C.V.M.; Silva, T.F.M.R.; Silveira, J.; Siqueira, J.V.; Carvalho, T.S.; Solar, R.R.C.; Tancredi, N.S.H.; Thomson, J.R.; Torres, P.C.; Vaz-de-Mello, F.Z.; Veiga, R.C.S.; Venturieri, A.; Viana, C.; Weinhold, D.; Zanetti, R.; Zuanon, J.A.S. 2013. A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B*, 368: 20120166.

Gascon, C.; Bierregaard, R.O.; Laurance, W.F.; Mérona, J.R. 2001. Deforestation and Forest Fragmentation in the Amazon. In: Bierregaard Jr., R.O.; Gascon, C.; Lovejoy, T.E.; Mesquita, R. (Eds.). *Lessons from Amazonia: the ecology and conservation of a fragmented forest*. Yale

University Press, USA, p. 22-30.

Gatz, A.J. 1979. Community organization in fishes as indicated by morphological features. *Ecology*, 60: 711-718.

Godar, J.; Gardner, T.A.; Tizado, J.; Pacheco, P. 2014. Actor-specific contributions to the deforestation slowdown in the Brazilian Amazon. *Proceedings of the National Academy of Sciences USA*, 111: 15591-15596.

Goulding, M.; Barthem, R.; Ferreira, E. 2003. *The Smithsonian atlas of the Amazon*. 1ra ed. Smithsonian Institution Press, Washington, 254p.

Grace, J.B. 2008. Structural equation modeling for observational studies. *Journal of Wildlife Management*, 72: 14-22.

Grace, J.B.; Youngblood, A.; Scheiner, S.M. 2009. Structural Equation Modeling and Ecological Experiments. In: Miao, S.; Carstenn, S.; Nungesser, M. (Eds.). *Real World Ecology: large-scale and long-term case studies and methods*. Springer Science, New York, USA, p.19-46.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86: 902-910.

Hansen, M.C.; Stehman, S.V.; Potapov, P.V.; Loveland, T.R.; Townshend, J.R.G.; DeFries, R.S.; Pittman, K.W.; Arunarwati, B.; Stolle, F.; Steininger, M.K.; Carroll, M.; DiMiceli, C. 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *Proceedings of the National Academy of Sciences USA*, 105: 9439-9444.

Hansen, M.C.; Stehman, S.V.; Potapov, P.V. 2010. Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences USA*, 107: 8650-8655.

Harnik, P.G.; Simpson, C.; Payne, L. 2012. Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society B*, 279: 4969-4976.

- Hector, A.; Bagchi, R. 2007. Biodiversity and ecosystem multifunctionality. *Nature*, 448: 188-190.
- Hercos, A.P.; Sobansky, M.; Queiroz, H.L.; Magurran, A.E. 2012. Local and regional rarity in a diverse tropical fish assemblage. *Proceedings of the Royal Society B*, 280: 20122076.
- Hillebrand, H.; Bennett, D.M.; Cadotte, M.W. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, 89: 1510-1520.
- Hoeinghaus, D.J.; Winemiller, K.O.; Birnbaum, J.S. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *Journal of Biogeography*, 34: 324-338.
- Hooper, D.U.; Chapin, F.S.; Ewel, J.J.; Hector, A.; Inchausti, P.; Lavorel, S.; Lawton, J.H.; Lodge, D.M.; Loreau, M.; Naeem, S.; Schmid, B.; Setälä, H.; Symstad, A.J.; Vandermeer, J.; Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75: 3-35.
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, 392p.
- Hubbell, S.P. 2013. Tropical rain forest conservation and the twin challenges of diversity and rarity. *Ecology and Evolution*, 3: 3263-3274.
- Hughes, R.M.; Rinne, J.N.; Calamusso, B. 2005. Historical changes in large river fish assemblages of the Americas: a synthesis. In: Rinne, J.N.; Hughes, R.M.; Calamusso, B. (Eds.). *Historical changes in large river fish assemblages of the Americas*. American Fisheries Society, Bethesda, USA, p.603-612.
- Hughes, R.M.; Wang, L.; Seelbach, P.W. 2006. *Landscape influences on stream habitat and biological assemblages*. Symposium 48, American Fisheries Society, Bethesda, USA, 698p.
- Hughes, R.M.; Peck, D.V. 2008. Acquiring data for large aquatic resource surveys: the art of compromise among science, logistics, and reality. *Journal of the North American*

Benthological Society, 27: 837-859.

INPE, 2013. Projeto PRODES: Monitoramento da floresta Amazônica Brasileira por satélite. (www.obt.inpe.br/prodes). Acesso em 06/06/2013.

Internationalrivers, 2013. (www.internationalrivers.org). Acesso em 20/05/2013.

Isbell, F.; Calcagno, V.; Hector, A.; Connolly, J.; Harpole, W.S.; Reich, P.B.; Scherer-Lorenzen, M.; Schmid, B.; Tilman, D.; van Ruijven, J.; Weigelt, A.; Wilsey, B.J.; Zavaleta, E.S.; Loreau, M. 2011. High plant diversity is needed to maintain ecosystem services. *Nature*, 477: 199-202.

IUCN, 2014. IUCN red list of threatened species. (www.iucnredlist.org). Acesso em 25/06/2014.

Jackson, D.A.; Peres-Neto, P.R.; Olden, J.D. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 157-170.

Jain, M.; Flynn, D.F.B.; Prager, C.M.; Hart, G.M.; DeVan, C.M.; Ahrestani, F.S.; Palmer, M.I.; Bunker, D.E.; Knops, J.M.H.; Jouseau, C.F.; Naeem, S. 2014. The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution*, 4: 104-112.

Johnson, P.T.J.; Hoverman, J.T.; McKenzie, V.J.; Blaustein, A.R.; Richgels, K.L.D. 2013. Urbanization and wetland communities: applying metacommunity theory to understand the local and landscape effects. *Journal of Applied Ecology*, 50: 34-42.

Junk, W.J. 1983. As águas da região Amazônica. In: Salati, E.; Schubart, H.O.R.; Junk, W.J.; Oliveira, A.E. (Eds.). *Amazônia: desenvolvimento, integração e ecologia*. CNPq/Brasiliense, São Paulo, p.45-100.

Junk, W.J.; Bayley, P.B.; Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication in Fisheries and Aquatic Sciences*, 106: 110-127.

Kark, S.; Mukerji, T.; Safriel, U.N.; Noy-Meir, I.; Nissani, R.; Darvasi, A. 2002. Peak morphological diversity in an ecotone unveiled in the chukar partridge by a novel estimator in a dependent sample (EDS). *Journal of Animal Ecology*, 71: 1015-1029.

Karpouzi, V.S.; Stergiou, K.I. 2003. The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology*, 62: 1353-1365.

Kasper, D.; Forsberg, B.R.F.; Amaral, J.H.F.; Leitão, R.P.; Py-Daniel, S.S.; Bastos, W.R.; Malm, O. 2014. Reservoir stratification affects methylmercury levels in river water, plankton, and fish downstream from Balbina hydroelectric dam, Amazonas, Brazil. *Environmental Science and Technology*, 48: 1032-1040.

Kaufmann, P.R.; Levine, P.; Robison, E.G.; Seeliger, C.; Peck, D.V. 1999. *Quantifying Physical Habitat in Wadeable Streams*. EPA/620/R-99/003. U.S. Environmental Protection Agency, Washington, 102p.

Kaufmann, P. R.; Larsen, D.P.; Faustini, J. 2009. Bed stability and sedimentation associated with human disturbances in pacific northwest streams. *Journal of the American Water Resources Association*, 45: 434-459.

Kaufmann, P.R.; Faustini, J. 2012. Simple measures of channel habitat complexity predict transient hydraulic storage in streams. *Hydrobiologia*, 685: 69-95.

Keenleyside, M.H.A. 1979. *Diversity and adaptation in fish behaviour*. Springer-Verlag, Berlin, 208p.

Kitajima, K.; Poorter, L. 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist*, 186: 708-721.

Kraft, N.J.B.; Godoy, O.; Levine, J.M. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences USA*, 112:

797-802.

Laliberté, E.; Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91: 299-305.

Lambim, E.F.; Meyfroidt, P. 2011. Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences USA*, 108: 3465-3472. doi:10.1073/pnas.1100480108

Laurance, W.F.; Peres, C. A. 2006. *Emerging Threats to Tropical Forests*. University of Chicago Press, Chicago, 520p.

Lavergne, S.; Thuiller, W.; Molina, J.; Debussche, M. 2005. Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. *Journal of Biogeography*, 32: 799-811.

Lavorel, S.; Grigulis, K.; McIntyre, S.; Williams, N.S.G.; Garden, D.; Dorrough, J., Berman, S.; Quétier, F.; Thébault, A.; Bonis, A. 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology*, 22: 134-147.

Leibold, M.A.; Holyoak, M.; Mouquet, N.; Amarasekare, P.; Chase, J.M.; Hoopes, M.F.; Holt, R.D.; Shurin, J.B.; Law, R.; Tilman, D.; Loreau, M.; Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7: 601-613.

Leprieur, F.; Beauchard, O.; Blanchet, S.; Oberdorff, T.; Brosse, S. 2008. Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology*, 6(2): e28. doi:10.1371/journal.pbio.0060028

Limburg, K.E.; Hughes, R.M.; Jackson, D.C.; Czech, B. 2011. Population increase, economic growth, and fish conservation: collision course or savvy stewardship? *Fisheries*, 36: 27-35.

Lomnický, G.A.; Whittier, T.R.; Hughes, R.M.; Peck, D.V. 2007. Distribution of nonnative aquatic vertebrates in western U.S. streams and rivers. *North American Journal of Fisheries*

Management, 27: 1082-1093.

Loreau, M.; Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412: 72-76.

Loreau, M.; de Mazancourt, C. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters*, 16: 106-115.

Lorion, C.M.; Kennedy, B.P. 2009. Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams. *Ecological Applications*, 19: 468-479.

Lyons, J.; Navarro-Pérez, S.; Cochran, P.A.; Santana, E.; Guzmán-Arroyo, M. 1995. Index of biotic integrity based on fish assemblages for the conservation of streams and rivers in west-central Mexico. *Conservation Biology*, 9: 569-584.

Lyons, K.G.; Schwartz, M. 2001. Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters*, 4: 358-365.

Lyons, K.G.; Brigham, C.A.; Traut, B.H.; Schwartz, M.W. 2005. Rare species and ecosystem functioning. *Conservation Biology*, 19: 1019-1024.

Mace, G.; Collar, N.; Gaston, K.; Hilton-Taylor, C.; Akcakaya, H.; Leader-Willimas, N.; Milner-Gulland, E.; Stuart, S. 2008 Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, 22: 1424-1442. doi:10.1111/j.1523-1739.2008.01044.x

Magurran, A.E. 2009. Threats to freshwater fish. *Science*, 325: 1215-1216.

Malhi, Y.; Roberts, J.T.; Betts, R.A.; Killeen, T.J.; Li, W.; Nobre, C.A. 2007. Climate change, deforestation and the fate of the Amazon. *Science*, 319: 169-172. doi:10.1126/science.1146961

- Mantyka-Pringle, C.; Martin, T.G.; Moffatt, D.B.; Linke, S.; Rhodes, J.R. 2014. Understanding and predicting the combined effects of climate change and land-use change on freshwater macroinvertebrates and fish. *Journal of Applied Ecology*, 51: 572-581.
- Marzin, A. P.; Verdonshot, P.; Pont, D. 2012. The relative influence of catchment, riparian corridor and local anthropogenic pressures on fish and macroinvertebrate assemblages in French rivers. *Hydrobiologia*, 704: 375-388.
- Mason, N.W.H.; MacGillivray, K.; Steel, J.B.; Wilson, J.B. 2003. An index of functional diversity. *Journal of Vegetation Science*, 14: 571-578.
- Mason, N.W.H.; Mouillot, D.; Lee, W.G.; Wilson, J.B. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111: 112-118.
- Matthews, W.J. 1998. *Patterns in freshwater fish ecology*. Chapman and Hall, New York, 756p.
- McGill, B.J.; Enquist, B.J.; Weiher, E.; Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21: 178-185.
- Mendonça, F.P.; Magnusson, W.E.; Zuanon, J. 2005. Relationships Between Habitat Characteristics and Fish Assemblages in Small Streams of Central Amazonia. *Copeia*, 4: 750-763.
- Mi, X.; Swenson, N.G.; Valencia, R.; Kress, W.J.; Erickson, D.L.; Pérez, A.J.; Ren, H.; Su, S.; Gunatilleke, N.; Gunatilleke, S.; Hao, Z.; Ye, W.; Cao, M.; Suresh, H.S.; Dattaraja, H.S.; Sukumar, R.; Ma, K. 2012. The contribution of rare species to community phylogenetic diversity across a global network of forest plots. *The American Naturalist*, 180: E17-E30.
- Morley, R.J. 2000. *Origin and Evolution of Tropical Rain Forests*. John Wiley & Sons Ltd., West Sussex, 378p.

Mouillot, D.; Mason, W.H.N.; Dumay, O.; Wilson, J.B. 2005. Functional regularity: a neglected aspect of functional diversity. *Oecologia*, 142: 353-359.

Mouillot, D. ; Villéger, S. ; Scherer-Lorenzen, M. ; Mason, N.W.H. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, 6: e17476.

Mouillot, D.; Bellwood, D.R.; Baraloto, C.; Chave, J.; Galzin, R.; Harmelin-Vivien, M.; Kulbicki, M.; Lavergne, S.; Lavorel, S.; Mouquet, N.; Paine, C.E.T.; Renaud, J.; Thuiller, W. 2013a. Rare species support vulnerable functions in high-diversity ecosystems. *PLOS Biology*, 11: e1001569.

Mouillot, D.; Graham, N.A.J.; Villéger, S.; Mason, N.W.H.; Bellwood, D.R. 2013b. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, 28: 167-177.

Naeem, S.; Duffy, J.E.; Zavaleta, E. 2012. The functions of biological diversity in an age of extinction. *Science*, 336: 1401-1406.

Nepstad, D.C.; Verissimo, A.; Alencar, A.; Nobre, C.; Lima, E.; Lefebvre, P.; Schlesinger, P.; Potter, C.; Moutinho, P.; Mendoza, E.; Cochrane, M.; Brooks, V. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, 398: 505-508.

Niinemets, U. 1999. Components of leaf dry mass per area – thickness and density – alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist*, 144: 35-47.

Nislow, K.H.; Hudy, M.; Letcher, B.H.; Smith, E.P. 2011. Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. *Freshwater Biology*, 56: 2135-2144.

Nunes, S.S.; Barlow, J.; Gardner, T.A.; Siqueira, J.V.; Sales, M.R.; Souza Jr., C.M. 2014. A 22 year assessment of deforestation and restoration in riparian forests in the eastern Brazilian Amazon. *Environmental Conservation*, DOI:10.1017/S0376892914000356.

Olden, J.D.; Poff, N.L.; Bestgen, K.R. 2008. Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology*, 89: 847-856.

Onoda, Y.; Westoby, M.; Adler, P.B.; Choong, A.M.F.; Clissold, F.J.; Cornelissen, J.H.C.; Díaz, S.; Dominy, N.J.; Elgart, A.; Enrico, L.; Fine, P.V.; Howard, J.J.; Jalili, A.; Kitajima, K.; Kurokawa, H.; McArthur, C.; Lucas, P.W.; Markesteijn, L.; Pérez-Harguindeguy, N.; Poorter, L.; Richards, L.; Santiago, L.S.; Sosinski Jr, E.E.; Van Bael, S.A.; Warton, D.I.; Wright, I.J.; Wright, S.J.; Yamashita, N. 2011. Global patterns of leaf mechanical properties. *Ecology Letters*, 14: 301-312.

Paine, C.E.T.; Stahl, C.; Courtois, E.A.; Patino, S.; Sarmiento, C.; Baraloto, C. 2010. Functional explanations for variation in bark thickness in tropical rain forest trees. *Functional Ecology*, 24: 1202-1210.

Peck, D.V.; Herlihy, A.T.; Hill, B.H.; Hughes, R.M.; Kaufmann, P.R.; Klemm, D.J.; Lazorchak, J.M.; McCormick, F.H.; Peterson, S.A.; Ringold, P.L.; Magee, T.; Cappaert, M. 2006. *Environmental Monitoring and Assessment Program: Surface Waters Western Pilot Study - field operations manual for wadeable streams. EPA620/R-06/003*. U.S. Environmental Protection Agency, Washington, 242p.

Peres, C.A.; Gardner, T.A.; Barlow, J.; Zuanon, J.; Michalski, F.; Lees, A.C.; Vieira, I.C.G.; Moreira, F.M.S.; Feeley, K.J. 2010. Biodiversity conservation in human-modified Amazonian forest landscapes. *Biological Conservation*, 143: 2314-2327.

Perkin, J.S.; Gido, K. 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecological Applications*, 22: 2176-1287.

Petchey, O.L.; Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5: 402-411.

Petchey, O.L.; Hector, A.; Gaston, K.J. 2004. How do different measures of functional diversity perform? *Ecology*, 85: 847-857.

Pitman, N.C.A.; Terborgh, J.; Silman, M.R.; Nunez, P. 1999. Tree species distributions in an

upper Amazonian forest. *Ecology*, 80: 2651-2661.

Power, M.E.; Tilman, D.; Estes, J.A.; Menge, B.A.; Bond, W.J.; Mills, L.S.; Daily, G.; Castilla, J.C.; Lubchenco, J.; Paine, R.T. 1996. Challenges in the quest for keystones. *Bioscience*, 46: 609-620.

Purvis, A.; Agapow, P.M.; Gittleman, J.C.; Mace, G.M. 2000. Non-random extinction and the loss of evolutionary history. *Science*, 288: 328-330.

Queiroz, L.J.; Torrente-Vilara, G.; Ohara, W.M.; Pires, T.H.S.; Zuanon, J.; Doria, C.R.C. 2013. *Peixes do rio Madeira*. Santo Antônio Energia, São Paulo.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing (www.R-project.org). Último acesso em 19/12/2014.

Rabinowitz, D. 1981. Seven forms of rarity. In: Synge, J. (Ed.). *The biological aspects of rare plant conservation*. Willey, New York, USA, p.205-217.

Reich, P.B.; Walters, M.B.; Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA*, 94: 13730-13734.

Ricklefs, R.E. 2000. Rarity and diversity in Amazonian forest trees. *Trends in Ecology and Evolution*, 15: 83-84.

Ricklefs, R. 2003. A comment on Hubbell's zero-sum ecological drift model. *Oikos*, 100: 185-192.

Riseng, C.M.; Wiley, M.J.; Black, R.W.; Munn D. 2011. Impacts of agricultural land use on biological integrity: a causal analysis. *Ecological Applications*, 21: 3128-3146.

Roth, N.E.; Allan, J.D.; Erickson, D.L. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology*, 11: 141-56

Sazima, I. 1986. Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology*, 29: 53-65.

Sazima, I.; Carvalho, L.N.; Mendonça F.P.; Zuanon, J. 2006. Fallen leaves on the water-bed: diurnal camouflage of three night active fish species in an Amazonian streamlet. *Neotropical Ichthyology*, 4(1): 119-122.

Sekercioglu, C.H.; Schneider, S.H.; Fay, J.P.; Loarie, S.R. 2008. Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, 22: 140-150.

Shipley, B. 2000. *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge, 330p.

Sibbing, F.A.; Nagelkerke, L.A.J. 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries*, 10: 393-437.

Soares-Filho, B.; Rajão, R.; Macedo, M.; Carneiro, A.; Costa, W.; Coe, M.; Rodrigues, H.; Alencar, A. 2014. Cracking Brazil's Forest Code. *Science*, 344: 363-364.

ter Steege, H.; Pitman, N.C.A.; Sabatier, D.; Baraloto, C.; Salomão, R.P.; Guevara, J.E.; Phillips, O.L.; Castilho, C.V.; Magnusson, W.E.; Molino, J.F.; Monteagudo, A.; Núñez Vargas, P.; Montero, J.C.; Feldpausch, T.R.; Coronado, E.N.H.; Killeen, T.J.; Mostacedo, B.; Vasquez, R.; Assis, R.L.; Terborgh, J.; Wittmann, F.; Andrade, A.; Laurance, W.F.; Laurance, S.G.W.; Marimon, B.S.; Marimon, B.H.; Vieira I.C.G.; Amaral, I.L.; Brienen, R.; Castellanos, H.; López D.C.; Duivenvoorden, J.F.; Mogollón, H.F.; Matos, F.D.A.; Dávila, N.; García-Villacorta, R.; Diaz P.R.S.; Costa, F.; Emilio, T.; Levis, C.; Schiatti, J.; Souza, P.; Alonso, A.; Dallmeier, F.; Montoya, A.J.D.; Piedade, M.T.; Araujo-Murakami, A.; Arroyo, L.; Gribel, R.; Fine, P.V.A.; Peres, C.A.; Toledo, M.; Aymard, C.G.A.; Baker, T.R.; Cerón, C.; Engel, J.; Henkel, T.W.; Maas, P.; Petronelli, P.; Stropp, J.; Zartman, C.E.; Daly, D.; Neill, D.; Silveira, M.; Paredes, M.R.; Chave, J.; Lima Filho, D.A.; Jørgensen, P.M.; Fuentes, A.; Schöngart, J.; Valverde, F.C.; Di Fiore, A.; Jimenez, E.M.; Mora, M.C.P.; Phillips, J.F.; Rivas, G.; van Andel, T.R.; von Hildebrand, P.; Hoffman, B.; Zent, E.L.; Malhi, Y.; Prieto, A.; Rudas, A.; Ruschell, A.R.; Silva, N.; Vos, V.; Zent, S.; Oliveira, A.A.; Schutz, A.C.;

Gonzales, T.; Nascimento, M.T.; Ramirez-Angulo, H.; Sierra, R.; Tirado, M.; Medina, M.N.U.; van der Heijden, G.; Vela, C.I.A.; Torre, E.V.; Vriesendorp, C.; Wang, O.; Young, K.R.; Baider, C.; Balslev, H.; Ferreira, C.; Mesones, I.; Torres-Lezama, A.; Giraldo, L.E.U.; Zagt, R.; Alexiades, M.N.; Hernandez, L.; Huamantupa-Chuquimaco, I.; Milliken, W.; Cuenca, W.P.; Pauletto, D.; Sandoval, E.V.; Gamarra, L.V.; Dexter, K.G.; Feeley, K.; Lopez-Gonzalez, G.; Silman, M.R. 2013. Hyperdominance in the Amazonian tree flora. *Science*, 342: 1243092.

Stropp, J.; ter Steege, H.; Malhi, Y. 2009. Disentangling regional and local tree diversity in the Amazon. *Ecography*, 32: 46-54.

Sutherland, A.B.; Mayer, J.L.; Gardiner, E.P. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology*, 47: 1791-1805.

Teresa, F.B.; Casatti, L. 2012. Influence of forest cover and mesohabitat types on functional and taxonomic diversity of fish communities in Neotropical lowland streams. *Ecology of Freshwater Fish*, 21: 433-442.

Terra, B.D.F.; Hughes, R.M.; Araujo, F.G. *In press*. Fish assemblages in Atlantic Forest streams: the relative influence of local and catchment environments on taxonomic and functional species. *Ecology of Freshwater Fish*.

Torrente-Vilara, G.; Zuanon, J.; Leprieur, F.; Oberdorff, T.; Tedesco, P.A. 2011. Effects of natural rapids and waterfalls on fish assemblage structure in the Madeira River (Amazon Basin). *Ecology of Freshwater Fish*, 20: 588-597.

Urban, M.C. ; Skelly, D.K. ; Burchsted, D. ; Price, W. ; Lowry, S. 2006. Stream communities across a rural-urban landscape gradient. *Diversity and Distributions*, 12: 337-350.

Villéger, S. ; Mason, N.W.H.; Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89: 2290-2301.

Villéger, S.; Miranda, J.R.; Hernandez, D.F.; Mouillot, D. 2010. Contrasting changes in

taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, 20: 1512-1522.

Vitousek, P.M.; Mooney, H.A.; Lubchenco, J.; Melillo, J.M. 1997. Human domination of Earth's ecosystems. *Science*, 277: 494-499.

Walser, C.A.; Bart, H.L. 1999. Influence of agriculture on instream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River System. *Ecology of Freshwater Fish*, 8: 237-246.

Wang, L.; Lyons, J.; Kanehl, P. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management*, 28: 255-266.

Wang, S.; Loreau, M. 2014. Ecosystem stability in space: α , β and γ variability. *Ecology Letters*, 17: 891-901.

Webb, P.W. 1984. Form and function in fish swimming. *Scientific American*, 251: 72-82.

Westcott, D.A.; Bentrupperbäumer, J.; Bradford, M.G.; McKeown, A. 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, 146: 57-67.

Whittier, T.R.; Stoddard, J.L.; Hughes, R.M.; Lomnický, G. 2006. Associations among catchment- and site-scale disturbance indicators and biological assemblages at least- and most-disturbed stream and river sites in the western USA. In: Hughes, R.M.; Wang, L.; Seelbach, P.W. (Eds.). *Landscape influences on stream habitat and biological assemblages*. Symposium 48, American Fisheries Society, Bethesda, USA, p.641-664.

Williams, S.E.; Middleton, J. 2008. Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions*, 14: 69-77.

Williams, S.E.; Williams, Y.M.; VanDerWal, J.; Isaac, J.; Shoo, L.P.; Johnson, C.N. 2009. Ecological specialization and population size in a biodiversity hotspot: how rare species avoid

extinction. *Proceedings of the National Academy of Sciences USA*, 106: 19737-19741.

Williams, S.E.; VanDerWal, J.; Isaac, J.; Shoo, L.P.; Storlie, C.; Fox, S.; Bolitho, E.E.; Moritz, C.; Hoskin, C.J.; Williams, Y.M. 2010. Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology*, 91: 2493.

Winemiller, K.O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 61: 343-365.

Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Cavender-Bares, J.; Chapin, T.; Cornelissen, J.H.C.; Diemer, M.; Flexas, J.; Garnier, E.; Groom, P.K.; Gulias, J.; Hikosaka, K.; Lamont, B.B.; Lee, T.; Lee, W.; Lusk, C.; Midgley, J.J.; Navas, M.L.; Niinemets, U.; Oleksyn, J.; Osada, N.; Poorter, H.; Poot, P.; Prior, L.; Pyankov, V.I.; Roumet, C.; Thomas, S.C.; Tjoelker, M.G.; Veneklaas, E.J.; Villar, R. 2004. The worldwide leaf economics spectrum. *Nature*, 428: 821-827.

Wright, I.J.; Reich, P.B.; Cornelissen, J.H.C.; Falster, D.S.; Garnier, E.; Hikosaka, K.; Lamont, B.B.; Lee, W.; Oleksyn, J.; Osada, N.; Poorter, H.; Villar, R.; Warton, D.I.; Westoby, M. 2005. Assessing the generality of global leaf trait relationships. *New Phytologist*, 166: 485-496.

Wright, I.J.; Ackerly, D.D.; Bongers, F.; Harms, K.E.; Ibarra-Manriquez, G.; Martinez-Ramos, M.; Mazer, S.J.; Muller-Landau, H.C.; Paz, H.; Pitman, N.C.A.; Poorter, L.; Silman, M.R.; Vriesendorp, C.F.; Webb, C.O.; Westoby, M.; Wright, S.J. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany*, 99: 1003-1015.

Zuanon, J.; Sazima, I. 2004. Natural history of *Stauroglanis gouldingi* (Siluriformes: Trichomycteridae), a miniature sand-dwelling candiru from central Amazonian streamlets. *Ichthyological Exploration of Freshwaters*, 15(3): 201-208.

Zuanon, J.; Sazima, I. 2005. Free meals on long-distance cruisers: the vampire fish rides giant catfishes in the Amazon. *Biota Neotropica*, 5: 109-114.

Zuanon, J.; Bockmann, F.A.; Sazima, I. 2006a. A remarkable sand-dwelling fish assemblage from central Amazonia, with comments on the evolution of psammophily in South American freshwater fishes. *Neotropical Ichthyology*, 4(1): 107-118.

Zuanon, J.; Carvalho, L.N.; Sazima, I. 2006b. A chamaleon characin: the plant-clinging and colour-charging *Ammocryptocharax elegans* (Characidiinae: Crenuchidae). *Ichthyological Explorations of Freshwaters*, 17(3): 225-232.

APPENDIX

PUBLICATION RELATED TO THE THESIS

rstb.royalsocietypublishing.org

Research



Cite this article: Gardner TA *et al.* 2013 A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Phil Trans R Soc B* 368: 20120166.
<http://dx.doi.org/10.1098/rstb.2012.0166>

One contribution of 18 to a Theme Issue 'Ecology, economy, and management of an agroindustrial frontier landscape in the south-east Amazon'.

Subject Areas:

ecology, environmental science

Keywords:

tropical forests, land use, sustainability, trade-offs, interdisciplinary research, social–ecological systems

Author for correspondence:

Toby A. Gardner
e-mail: tobyagardner@gmail.com

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rstb.2012.0166> or via <http://rstb.royalsocietypublishing.org>.

A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network

Toby A. Gardner^{1,2}, Joice Ferreira³, Jos Barlow², Alexander C. Lees⁴, Luke Parry², Ima Célia Guimarães Vieira⁴, Erika Berenguer², Ricardo Abramovay⁵, Alexandre Aleixo⁴, Christian Andretti⁶, Luiz E. O. C. Aragão⁷, Ivanei Araújo⁴, Williams Souza de Ávila⁸, Richard D. Bardgett², Mateus Batistella⁹, Rodrigo Anzolin Begotti¹⁰, Troy Beldini¹¹, Driss Ezzine de Blas¹², Rodrigo Fagundes Braga¹³, Danielle de Lima Braga¹³, Janaína Gomes de Brito⁶, Plínio Barbosa de Camargo¹⁴, Fabiane Campos dos Santos¹¹, Vívian Campos de Oliveira⁶, Amanda Cardoso Nunes Cordeiro¹⁵, Thiago Moreira Cardoso³, Déborah Reis de Carvalho¹³, Sergio André Castelan¹⁵, Júlio César Mário Chaul¹⁶, Carlos Eduardo Cerri¹⁰, Francisco de Assis Costa¹⁷, Carla Daniele Furtado da Costa¹⁵, Emilie Coudel^{3,12}, Alexandre Camargo Coutinho¹⁸, Dênis Cunha¹⁶, Álvaro D'Antona¹⁹, Joelma Dezincourt⁴, Karina Dias-Silva²⁰, Mariana Durigan¹⁰, Júlio César Dalla Mora Esquerdo¹⁸, José Feres²¹, Silvio Frosini de Barros Ferraz¹⁰, Amanda Estefânia de Melo Ferreira⁴, Ana Carolina Fiorini²², Lenise Vargas Flores da Silva¹¹, Fábio Soares Frazão¹³, Rachel Garrett²³, Alessandra dos Santos Gomes⁴, Karoline da Silva Gonçalves⁴, José Benito Guerrero²⁴, Neusa Hamada⁶, Robert M. Hughes²⁵, Danilo Carmago Iglori⁵, Ederson da Conceição Jesus²⁶, Leandro Juen¹⁷, Miércio Junior¹¹, José Max Barbosa de Oliveira Junior²⁷, Raimundo Cosme de Oliveira Junior³, Carlos Souza Junior²⁸, Phil Kaufmann²⁹, Vanesca Korasaki¹³, Cecília Gontijo Leal¹³, Rafael Leitão⁶, Natália Lima¹⁵, Maria de Fátima Lopes Almeida¹⁵, Reinaldo Lourival³⁰, Júlio Louzada¹³, Ralph Mac Nally³¹, Sébastien Marchand¹⁶, Márcia Motta Maués³, Fátima M. S. Moreira¹³, Carla Morsello³², Nárgila Moura⁴, Jorge Nessimian²², Sâmia Nunes²⁸, Victor Hugo Fonseca Oliveira¹³, Renata Pardini³³, Heloisa Correia Pereira¹⁹, Paulo Santos Pompeu¹³, Carla Rodrigues Ribas¹³, Felipe Rossetti¹⁰, Fernando Augusto Schmidt¹³, Rodrigo da Silva¹¹, Regina Célia Viana Martins da Silva³, Thiago Fonseca Morello Ramalho da Silva⁵, Juliana Silveira¹³, João Victor Siqueira²⁸, Teotônio Soares de Carvalho¹³, Ricardo R. C. Solar^{2,17}, Nicola Savério Holanda Tancredi¹⁷, James R. Thomson³¹, Patrícia Carignano Torres³³, Fernando Zagury Vaz-de-Mello³⁴, Ruan Carlo Stulpen Veiga³⁵, Adriano Venturieri³, Cecília Viana⁴, Diana Weinholt³⁶, Ronald Zanetti¹³ and Jansen Zuanon⁶

¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

²Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

³Embrapa Amazônia Oriental, Travessa Dr. Enéas Pinheiro s/n, CP 48, Belém, Pará 66.095-100, Brazil

⁴MCTI/Museu Paraense Emílio Goeldi, CP 399, CEP 66040-170, Belém, PA, Brazil

⁵Faculdade de Economia, Administração e Contabilidade, Av. Prof. Luciano Gualberto, Cidade Universitária, 05508-010, São Paulo, SP, Brazil

- ⁶INPA. Instituto Nacional de Pesquisas da Amazônia. Av. André Araújo, 2.936 - Petrópolis, 69080-971, Manaus, AM, Brazil
- ⁷College of Life and Environmental Sciences, University of Exeter, EX4 4RJ, UK
- ⁸Universidade Rural da Amazônia, Rodovia PA 256, km 06, Bairro Nova Conquista, s/n, 68625-000, Paragominas, PA, Brazil
- ⁹Embrapa Monitoramento por Satélite, Av. Soldado Passarinho, 303, Fazenda Chapadão, 13070-115, Campinas, SP, Brazil
- ¹⁰Universidade de São Paulo, Escola Superior de Agricultura "Luiz de Queiroz", Esalq/USP, Avenida Pádua Dias, 11, São Dimas, Piracicaba, SP, Brazil
- ¹¹Universidade Federal do Oeste do Pará, Rua Vera Paz, S/N, Bairro Salé, 68040-250, Santarém, PA, Brazil
- ¹²Centre de coopération internationale en recherche agronomique pour le développement - CIRAD. Campus International de Baillarguet. 34398 Montpellier Cedex 5, France
- ¹³Universidade Federal de Lavras, Campus Universitário, CP 3037, 37200-000, Lavras, MG, Brazil
- ¹⁴Centro de Energia Nuclear na Agricultura, CENA/USP, Universidade de São Paulo, Av. Centenário 303, São Dimas, Piracicaba, SP, Brazil
- ¹⁵Universidade do Estado do Pará, Rodovia PA-125, s/n, Bairro: Algelim, 68625-000, Paragominas, PA, Brazil
- ¹⁶Universidade Federal de Viçosa, Av. P. H. Rolfs, s/n, Centro, 36570-000, Viçosa, MG, Brazil
- ¹⁷Universidade Federal do Pará, Rua Augusto Corrêa, s/n, Campus Profissional II, Guamá, 66000-000, Belém, PA, Brazil
- ¹⁸Embrapa Informática Agropecuária, Av. André Tosello, 209, Barão Geraldo, 13083-886, Campinas, SP, Brazil
- ¹⁹Universidade Estadual de Campinas, Faculdade de Ciências Aplicadas, Rua Pedro Zaccharia, 1300, Cidade Universitária, 13484-350, Limeira, SP, Brazil
- ²⁰Universidade Federal de Goiás, Campus II, 74001-970, Goiânia, GO, Brazil
- ²¹Instituto de Pesquisa Econômica Aplicada, Avenida Presidente Antônio Carlos, 51, 17° andar, Centro, 20020-010, Rio de Janeiro, RJ, Brazil
- ²²Universidade Federal do Rio de Janeiro, CP 68501, 21941-972, Rio de Janeiro, RJ, Brazil
- ²³Stanford University, Energy and Environment Building, 4205, 473 Via Ortega, Stanford, CA 94305, California, USA
- ²⁴The Nature Conservancy, Av. Nazaré, 280, Bairro Nazaré, 66035-170, Belém, PA, Brazil
- ²⁵Amnis Opes Institute and Department of Fisheries & Wildlife, Oregon State University, 200 SW 35th St., Corvallis, OR 97333, USA
- ²⁶Embrapa Agrobiologia, BR 465, km 7, 23891-000, Seropédica, RJ, Brazil
- ²⁷Universidade do Estado de Mato Grosso (UNEMAT), Br 158, Km 148, 78690-000, Nova Xavantina, MT, Brazil
- ²⁸IMAZON, Rua Domingos Marreiros, 2020, 66060-160, Belém, PA, Brazil
- ²⁹U.S. Environmental Protection Agency Office of Research and Development, 200 S.W. 35th St., Corvallis, OR 97333, USA
- ³⁰Ministério de Ciência, Tecnologia e Inovação, Esplanada dos Ministérios, Bloco E, 70067-900, Brasília, DF, Brazil
- ³¹Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Victoria 3800, Australia
- ³²Escola de Artes, Ciências e Humanidades, Universidade de São Paulo, Rua Arlindo Bettio 1000, 03828-000 São Paulo, Brazil
- ³³Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, 101, 05508-090 São Paulo, Brazil
- ³⁴Universidade Federal Mato Grosso, Av. Fernando Correa da Costa, s/n, Coxipó, 78060-900, Cuiabá, MT, Brazil
- ³⁵Universidade Federal Fluminense, Rua Miguel de Frias, 9, Icaraí, 24220-900, Niterói, RJ, Brazil
- ³⁶Department of International Development, London School of Economics, Houghton Street, WC2A 2AE, London, UK

Science has a critical role to play in guiding more sustainable development trajectories. Here, we present the Sustainable Amazon Network (*Rede Amazônia Sustentável*, RAS): a multidisciplinary research initiative involving more than 30 partner organizations working to assess both social and ecological dimensions of land-use sustainability in eastern Brazilian Amazonia. The research approach adopted by RAS offers three advantages for addressing land-use sustainability problems: (i) the collection of synchronized and co-located ecological and socioeconomic data across broad gradients of past and

present human use; (ii) a nested sampling design to aid comparison of ecological and socioeconomic conditions associated with different land uses across local, landscape and regional scales; and (iii) a strong engagement with a wide variety of actors and non-research institutions. Here, we elaborate on these key features, and identify the ways in which RAS can help in highlighting those problems in most urgent need of attention, and in guiding improvements in land-use sustainability in Amazonia and elsewhere in the tropics. We also discuss some of the practical lessons, limitations and realities faced during the development of the RAS initiative so far.

1. Introduction

Land-use and land-cover change associated with agricultural expansion and intensification is the most visible indicator of the human footprint on the biosphere [1–3]. Ongoing land-use change is most acute in the tropics [4], with *ca* 50 000 km² p.a. of native vegetation being cleared [5]. These changes are driven by increasing resource demands from a larger and wealthier human population, coupled with the effects of increasing economic globalization and land scarcity [6]. The creation and strengthening of more sustainable development trajectories in the twenty-first century depends on our ability to balance rising demands for food, energy, natural resources and the alleviation of hunger and poverty with the protection and restoration of natural ecosystems, and the critical ecosystem services they provide [7,8].

Amazonia represents a major sustainability challenge: as well as being the world's largest remaining tropical forest, the entire Amazon biome is home to more than 30 million people and provides locally, regionally and globally significant human-welfare benefits, including economic goods (e.g. timber and agricultural products) and non-market ecosystem services, such as climatic regulation and biodiversity conservation [4,9,10]. Rapid social and ecological change has left the future of the Amazon region uncertain [11–13]. In the Brazilian Amazon, in particular, recent reductions in the rate of deforestation, expansion of protected areas, increased market-based demand for more responsible land-use practices, and a strengthening of local and regional governments and civil society organizations provide some cause for guarded optimism that the Amazon economy can be set on a sustainable footing [14–16]. However, we need to ensure the right choices are made as soon as possible, thereby reducing the likelihood of costly or potentially irreversible damage to both social and ecological systems in the region [12,17]. Science can help this process by identifying the problems that need to be addressed first, and assessing the long-term social and ecological implications of land-use alternatives in planning for both regional development and ecological conservation [2,18,19].

While there is already a substantial body of social and ecological knowledge on the Amazon [11,20–22], scientists are often criticized for failing to deliver the evidence most needed to foster sustainability [23]. Criticisms include the fragmented and disciplinary nature of many research projects, a narrow focus on specific ecological or social problems and spatial scales, and a weak connection to local actors and

institutions that are ultimately responsible for implementing changes in land-use policy and management [22–25].

Here, we present the work of the Sustainable Amazon Network (RAS; *Rede Amazônia Sustentável* in Portuguese), which is a multidisciplinary research initiative involving more than 30 research institutions and partner organizations. The overall aim of this paper is to present the conceptual and methodological basis of the RAS initiative while also discussing many fundamental challenges that confront research on land-use sustainability across the tropics. Building on the work of a number of earlier and groundbreaking interdisciplinary assessments in the Amazon, including the LBA (Programa de Grande Escala da Biosfera-Atmosfera na Amazônia) and GEOMA (Pesquisas de Desenvolvimento de Métodos, Modelos e Geoinformação para Gestão Ambiental) research programmes [11,21,26], RAS seeks to address some of the limitations listed above by assessing the sustainability of land-use systems in two dynamic regions of eastern Brazilian Amazonia. The research approach adopted by RAS offers three advantages for addressing this overarching goal: (i) the collection of synchronized and co-located ecological and socioeconomic data across broad gradients of past and present human use and exploitation of natural resources; (ii) a nested sampling design that allows comparisons of the ecological and socioeconomic conditions associated with different land uses to be made across local, landscape and regional scales; and (iii) a strong engagement with a wide variety of actors and non-research institutions.

Drawing upon the strengths of our approach, RAS aims to make important advances in understanding the sustainability challenges facing Amazonia with regards to four broad objectives. First, we aim to quantify and better understand the ecological consequences of forest clearance, forest degradation and exploitation, and agricultural change (including cattle farming and silviculture) at several spatial scales. We are particularly interested in assessing the relative importance of local- and landscape-scale variables, as well as the extent to which past human impacts can help explain observed patterns in current ecological condition. Our measures of ecological condition include changes in terrestrial and aquatic biodiversity, carbon stocks, soil chemical and physical condition and aquatic condition. Our second objective is to examine the factors that determine patterns of land use, management choice, agricultural productivity and profits (and hence opportunity costs for conservation) and patterns of farmer well-being. Beyond input cost, geophysical (e.g. soil type, topography) and location (e.g. road and market access) factors, we recognize the potential importance of social-cultural factors in influencing land-use behaviours, including geographical origin, technical support, credit access, social capital and the importance of supply chains. Third, we plan to use our multidisciplinary assessment to evaluate the relationships between conservation and development objectives and identify potential trade-offs and synergies. Here, we are interested in the relative ecological and socioeconomic costs and benefits of alternative land-use and management choices, and the potential for feedbacks, multiple scale interactions and dependencies and unintended ('perverse') outcomes. Last, RAS seeks to help enable future research initiatives to maximize their cost-effectiveness by examining the implications of choices made with respect to variable selection, sampling design, prioritization of research questions and analyses, and approaches for engaging with local actors and institutions and disseminating results.

The remainder of this paper focuses on describing the key methodological components and novel features of our research design. We highlight some of the practical lessons and realities faced during the development of the RAS initiative so far, and identify the possible ways in which RAS could have a lasting impact in guiding improvements in land-use sustainability in Amazonia and elsewhere in the tropics.

2. The Sustainable Amazon Network: research design

(a) A conceptual framework for assessing land-use sustainability

RAS is inspired by the now well-established paradigm of 'sustainability science'—a science that is focused explicitly on the dynamic interactions between nature and society and is committed to place-based and solution-driven research across multiple scales [27,28]. Making explicit our understanding of the interactions among and between social and ecological phenomena, and their relationship to an overarching sustainability agenda is critical to the effectiveness and transparency of such a research programme.

The challenge of realizing a more sustainable development trajectory for the Amazon region lies in identifying, protecting and restoring the balance of ecological and socioeconomic values necessary to maintain the flow of critical ecosystem services and adapt to changing conditions, while also safeguarding the ability to exploit new opportunities for human development. The starting point for any research programme on sustainability is the selection of a set of socio-ecological values that can provide a basis for assessment. Our focus in RAS is on the conservation of forest-dependent biodiversity (terrestrial and aquatic), the conservation and enhancement of carbon stocks, soil and water quality, the provision of agricultural, silvicultural, timber and non-timber forest products, and the protection and betterment of human well-being.

From this basis, the RAS research process can then address our primary objectives in helping to quantify and understand some of the social and ecological problems and trajectories faced by the Amazon region, examine interactions and the potential for costly or potentially irreversible impacts, and evaluate the social and ecological costs, benefits and trade-offs associated with proposed management interventions. We view the transition towards sustainability as a guiding vision for continuous improvements in management practices rather than a search for a static blueprint of best practice techniques. Within this framework, we see the role of research as providing both an ongoing measure of management performance and a laboratory for testing new ideas for positive change.

Building on earlier work by Collins *et al.* [19], we present a simple framework of how we view the interacting components of our social-ecological study system, and the hypothesized cause-effect relationships, assumptions and feedbacks that provide a foundation for setting specific research objectives (figure 1). Outcomes measures (i.e. changes in valued attributes, such as native biodiversity, ecosystem service provision and human well-being) are captured in both the social and the ecological dimensions, and through changes in the stocks and flows of ecosystem services. Effects on these measures are felt through the cascading effects of changes in human behaviour

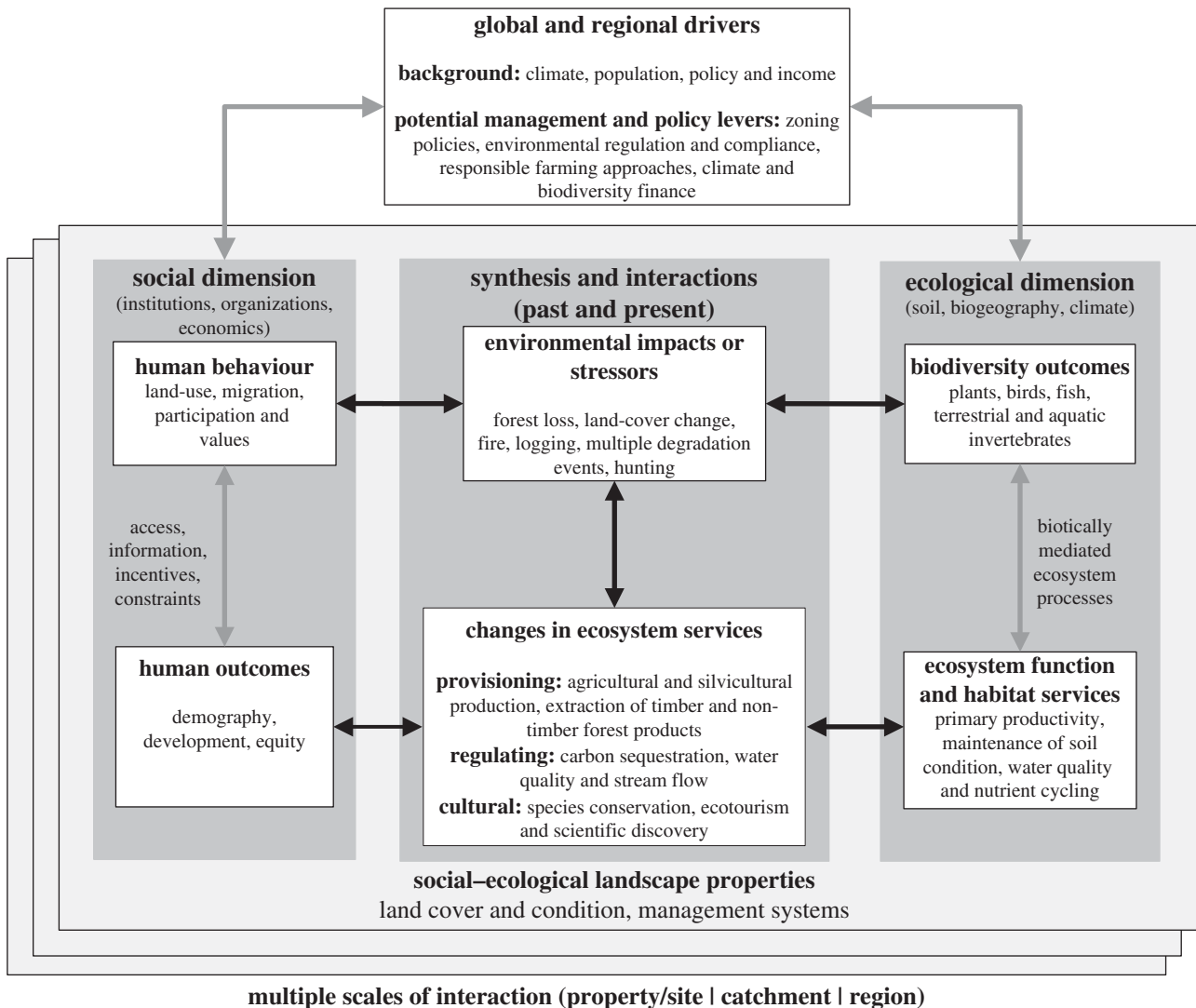


Figure 1. Conceptual model of study system under investigation by the Sustainable Amazon Network. Adapted from a generic framework presented in Collins *et al.* [19] to illustrate how we view the interacting components of our social–ecological study system, and the hypothesized cause–effect relationships, contexts (social and ecological dimensions and social–ecological interactions), assumptions and feedbacks between outcome measures (e.g. related to human well-being, biodiversity and ecosystem service provision), impacts and social and ecological processes, which together provide a foundation for setting specific research objectives. Not all influences and feedbacks are of equal importance and no attempt is made in the model to distinguish relative effect sizes. Social–ecological landscape properties are emergent and dynamic changes in landscape features that mediate relationships between social and ecological phenomena. System dynamics play out across multiple spatial scales. Variables listed are those that have been studied by RAS.

and associated environmental impacts on landscape properties and ecosystem functions. Each one of the influence arrows in figure 1 encompasses a set of specific, disciplinary research questions. The importance of diverse human impacts (both faster dynamics (such as fire and logging) and slower dynamics (such as cumulative land-use change and repeated degradation events)) in determining changes in outcome variables is examined using a space-for-time substitution across a highly replicated network of sampling locations and landholdings, coupled with detailed remotely sensed time-series analysis of past land-cover change and forest degradation. A focus of our work is understanding the extent to which landscape properties (often measurable from satellite and secondary data alone and used to compare multiple landscapes) can provide adequate proxies for understanding changes in the sustainability trajectory of the system as a whole. As much as possible, we try to ensure that the interpretation of our results takes account of the spatial scale of observation, and unmeasured factors, including the effects of external drivers such as climate change and global markets, on the study system. Last, we seek to characterize the effects

of a set of potential management and policy levers on the long-term dynamics and outcomes of the study system (figure 1).

(b) Key RAS design features

RAS is an example of a research initiative that collects matched social and ecological data at multiple scales and of relevance to multiple sustainability problems (see also [29]). A number of features of the research design adopted by RAS offer clear advantages for addressing questions about land-use sustainability and management.

(i) Spatial scale of assessment

Much of the existing social and ecological research in the Amazon (and elsewhere) has not been conducted at the most relevant spatial scales for assessing and guiding the development of more sustainable land-use strategies. Research has concentrated either on the entire Amazon basin, which often depends upon very coarse-scale data and obscures critically important inter- and intra-regional processes and interactions

[30], or on detailed work on a few intensively studied research sites, which captures only a tiny fraction of the variability in environmental and land-use gradients that drive much social and ecological change (see [10] in the case of biodiversity research). While both large- and small-scale research is necessary, much more work is needed at the 'mesoscale' level (i.e. spanning hundreds of kilometres and coincident with the scale of individual municipalities in Brazil). The RAS assessment was conducted in two study regions in the Brazilian state of Pará: the municipality of Paragominas (1.9 million hectares) and part of the municipalities of Santarém and Belterra (ca 1 million hectares) (figure 2). There are several important advantages to working at this spatial scale. The socioeconomic and ecological data collected by RAS cover broad gradients of change in both ecological (e.g. natural factors, such as soil type and the extent of forest loss, degradation and land-use intensification) and socioeconomic variables (e.g. rural population density, property size, wealth and market access), thereby affording more confidence in the general relevance of the patterns, drivers and trade-offs inferred from sample data [31]. In addition, a focus at the mesoscale facilitates assessment of the importance of both local (farm) and regional (state and biome) processes and objectives in a way that work focused on either smaller or larger scales cannot readily achieve. Finally, municipalities (or the equivalent scale of administration elsewhere) are also the administrative unit with arguably the greatest awareness of local pressures on natural resources and social services, and the greatest responsibility for institutional linkages between local communities and states or regions [30].

(ii) Choice of study regions

The RAS study regions of Paragominas and Santarém–Belterra differ both biophysically and in their histories of human occupation and use. By collecting data from two distinct regions of eastern Amazonia, we have a rare opportunity to better understand the extent to which inferences derived from one region can be generalized to another.

The modern city of Santarém, once a centre of pre-Colombian civilization, was founded in 1661, whereas Paragominas was founded as recently as 1959. Recent development of both regions has been closely associated with the construction of federal highways. Northern Santarém and neighbouring Belterra have been densely settled by small-scale farmers for more than a century. By contrast, Paragominas had a very low population density prior to its colonization by cattle ranchers from southern Brazilian states in the 1950s and 1960s, and the boom in the timber industry during the 1980s and 1990s. Both regions are relatively consolidated, with decreasing rates of deforestation of primary vegetation, although on-going paving of the highway means southern Santarém will probably experience both increased human colonization and agricultural expansion in the near future. Large-scale, mechanized agriculture became established in both regions only in the early 2000s and has increased rapidly in recent years (usually at the expense of both pastures and secondary forest), currently occupying approximately 40 000 and 60 000 ha in Santarém and Paragominas, respectively. Paragominas has also witnessed a rapid recent expansion of silviculture (mostly *Eucalyptus* spp. and *Schizolobium amazonicum*). Both regions are distinct from the agro-industrial frontier in Mato Grosso which is dominated by large-scale mechanized farming primarily for export [32,33]. Although mechanized farming is expanding rapidly in both

study regions, in contrast to Mato Grosso, the majority of properties are less than 1000 ha. Moreover, local and regional urban centres still provide significant markets for cattle, and landscapes are interspersed with a diverse array of densely populated small-holder colonies and agrarian reform settlements.

Both Santarém and Paragominas have recently embarked upon high-visibility, multi-sectoral sustainability initiatives; specifically, a moratorium on expansion of soya bean from deforested areas in Santarém, and the foundation of the *Município Verde* (Green County) initiative for promoting sustainable land-use systems in Paragominas. These processes have strong support from non-governmental organizations, farmer's unions and local government, and have facilitated the development of RAS by helping us gain trust with local actors and institutions, tailoring the research planning and design towards local priorities and needs, and increasing receptivity towards project results and recommendations.

It is not viable to repeat the scale of assessment of the RAS initiative in every tropical forest region around the world. However, by working at multiple scales and in two differing municipalities that encompass many characteristics of eastern Amazonia and elsewhere, such as large areas of extensive cattle pasture, emergent mechanized agriculture and a population that is highly mobile and dominated by small-holder farmers, we believe that our results provide a suitable laboratory for better understanding many of the risks and opportunities facing the development of more sustainable landscapes across the wider region. By concentrating our efforts in two regions that have received particular attention from existing initiatives in sustainable land use, our results almost certainly will receive greater exposure to, and engagement with, a wide range of decision makers. Last, a key focus of our work is to employ our uniquely comparable and diverse datasets to identify a subset of cost-effective ecological and social indicators that can help guide applied research and monitoring work in other study regions.

(iii) Sampling design

The RAS sampling design is based on a sample of 18 third- or fourth-order hydrological catchments (ca 5000 ha) in each region. Catchments are distributed over a gradient of forest cover in 2009 (10–100% in Santarém; 6–100% in Paragominas; figure 2), with detailed ecological and socioeconomic information being collected from study transects and individual farms within each catchment (figure 2; electronic supplementary material). Advantages to this nested design include the potential for determining the relative importance of drivers and constraints that operate at different spatial scales, and the capacity to make connections between local/individual (farm) and larger scale/public (municipality and state) conservation and development objectives (table 1). Sampling at the catchment scale also permits the integration of terrestrial and aquatic information, and the assessment of changes in ecological and socioeconomic variables that are highly correlated at local scales, such as cumulative deforestation, economic activities and human population density. The 36 study catchments (figure 2; electronic supplementary material, figures S1 and S2) were selected to capture the full deforestation gradient, while incorporating priority areas identified by members of the municipal governments and farming communities (e.g. agrarian reform settlements, traditional rural communities and areas of recent agricultural expansion and development).

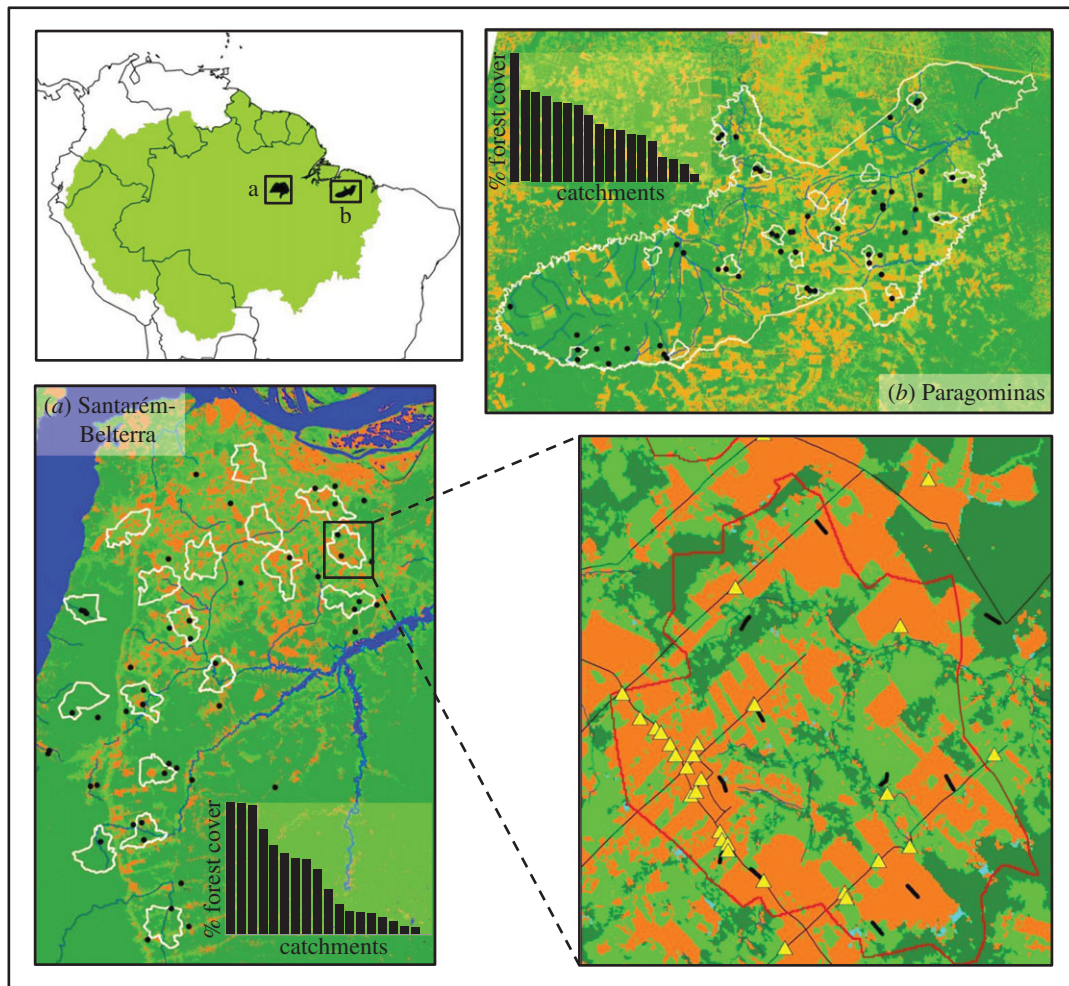


Figure 2. The Sustainable Amazon Network nested sampling design. Distribution of study catchments (white) is shown within both Paragominas (*a*) and Santarém-Belterra (*b*). Black circles show location of streams sampled during the aquatic assessment. Black bar charts show distribution of remnant forest cover across catchments. (*c*) The distribution of study transects (black lines) and the principal household of producer landowners (triangles) in the catchment of Boa Esperança in Santarém. Land-use classification derived from Landsat 2010 image, showing primary forest (grey), secondary forest (light grey), deforested areas (white) and major water bodies (dark grey). (Online version in colour.)

Ecological data were collected from a sample of 300 m study transects in every catchment, distributed using a stratified-random sampling design, where a standard density of transects (1 per 400 ha) was distributed across the catchment in proportion to the percentage cover of total forest and production areas (encompassing agriculture, pasture, fructiculture and silviculture; figure 2). For example, if half of the landscape was covered by forest, then half of the transects were allocated to forest. In catchments with very low levels of forest cover we sampled additional forest transects to ensure a minimum sample of three transects in all catchments. Within each of these two land-use categories (forest and non-forest), sample transects were distributed randomly with a minimum separation of 1500 m to minimize spatial dependence. The use of this stratified-random sampling design provided a balance between the need for: (i) proportional sampling of forest and non-forest areas, and a sufficient density and coverage of sample points to capture major differences in landscape structure and composition among different catchments; and (ii) a well-dispersed set of sampling points across forest and non-forest areas that captured important environmental heterogeneities within each catchment and across the region as a whole, helping to minimize problems of pseudo-replication. Aquatic sampling was conducted across 50 stream sites, each 150 m long in each region, with samples distributed

along a gradient of prior human impact based primarily on the amount of remnant forest cover in the upstream catchment (and not constrained to terrestrial study catchments).

Socioeconomic data were collected from all rural properties with an ecological study transect. Owing to the stratified design, transects tended to be in larger properties and under-represent smaller farms. Therefore, we mapped all rural producers in each catchment and sub-sampled a maximum of 20 randomly selected properties (with at least 1 ha and producing in 2009). Given our focus on the producer community, this sample excluded urban and periurban areas, but could include some of the same farms in the transect-based sample. This combination of sampling techniques enables us to describe the dominant socioeconomic and demographic characteristics of different producers, and to provide a detailed socioeconomic profile of the farming population in each catchment (figure 2). Where rural properties had more than one household (e.g. where there are workers or relatives living on the property), additional surveys on household demography, origins and well-being were made according to the total number of residences (table 1).

(iv) Social and ecological field sampling

RAS project members conducted a detailed assessment of ecological and socioeconomic patterns and processes in

Table 1. Remote-sensing, socioeconomic and environmental data sampled by the Sustainable Amazon Network.

variable type	variables	summary characteristics			
		Paragominas		Santarém	
remote sensing	biannual land-use classification (since 1988 in Paragominas and 1990 in Santarém-Belterra); age of deforestation; frequency and timing of forest degradation events; age and frequency of secondary forest regeneration; mapping of fire and logging scars; indices of deforestation and forest regeneration trajectories; cover of mechanized agriculture since 2000 (MODIS images); land-use intensity by hydrological distances between stream networks and forest remnants				
socioeconomic	property sizes in socioeconomic survey	number	area surveyed (ha)	number	area surveyed (ha)
	0–25 ha	44	936	150	1656
	25–100 ha	47	3030	110	7587
	100–300 ha	20	3577	20	3837
	300–1000 ha	16	9222	21	12 397
	over 1000 ha	44	238 979	16	62 978
	total number of properties	171	255 744	317	88 455
	total number of households	223		400	
	survey modules	property characteristics; household characteristics, demography and well being; productivity and inputs of different production systems; fire use and impacts; forest use (and hunting)			
soil	physical structure, soil fertility, total C and N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, phospholipid fatty acids (PLFA) analysis of soil microbes, microbial biomass, soil water soluble nutrients, soil emissions of CO_2 , NH_4 , N_2O	3120 and 2580 soil samples from Paragominas and Santarém, respectively. Five replicates from each transect and at three depths (0–10, 10–20, 20–30 cm). Microbial and PLFA data, soil water soluble nutrients and soil gases emissions for selected catchments from Santarém only.			
vegetation and carbon stocks	biomass and vegetation structure (including dead wood, leaf litter and structural measurements)	44 359 stems measured and identified		38 584 stems measured and identified	
	tree, liana and palm diversity	1052 species		1118 species	
	disturbance	observations of fire and logging scars and other damage on all stems			
terrestrial fauna	birds	364 species		377 species	
	dung beetles	85 species		99 species	
		53 113 specimens		40 664 specimens	
	ants	ca 300 species		430 species	
	orchid bees	28 species		34 species	
	ecosystem functions	n.a.		dung removal, soil turbation, and seed dispersal by dung beetles, and seed predation by ants	
aquatic system	physical habitat	237 measurements relating to channel morphology, substrate, habitat complexity and cover, riparian vegetation, channel–riparian interactions and disturbance			
	aquatic quality	physical and chemical parameters of water (dissolved oxygen, conductivity, pH, temperature, nitrate and ammonia)			

(Continued.)

Table 1. (Continued.)

variable type	variables	summary characteristics	
		Paragominas	Santarém
	fish	112 species	71 species
		18 669 individuals	7990 individuals
	Ephemeroptera, Plecoptera and Trichoptera	49 genera	54 genera
		14 113 individuals	7937 individuals
	Heteroptera	9 genera	14 genera
		1847 individuals	543 individuals
	Odonata	97 species	68 species
		1990 individuals	1849 individuals

both study regions between April 2010 and August 2011 (table 1 and figure 2; electronic supplementary material). Choices of sample variables and methods were based on our research priorities, cost-effectiveness and the need to collect a large number of representative samples [34] (table 1). Sampling of terrestrial biodiversity focused on trees and lianas, birds, dung beetles, ants, orchid bees and soil microbes. In a subset of catchments, additional measurements were made of ecosystem functions mediated by beetles and ants (including dung burial, seed dispersal and seed predation). Aquatic biodiversity (and metrics of aquatic condition) consisted of fish and macroinvertebrate assemblages (table 1). Ecosystem service supply was measured for carbon stocks (above- and below-ground) and the maintenance of soil condition (physical and chemical properties). The habitat structure of both terrestrial and aquatic environments was assessed using a combination of measures of canopy openness, vegetation structure, dead wood and leaf litter, and the morphology and substrate of stream channels. Socioeconomic data were collected on the characteristics of study properties (such as land cover, legal status) and producer households (including household demography, producer origins, income, access to services, subjective measures of well-being), costs and productivity of different production systems (livestock, arable and perennial crops, silviculture and timber harvesting), fire use and effects, and the benefits and costs of maintaining forest reserves (including the extraction of timber and non-timber forest products, and risks of invasion and theft) (table 1).

Legacy effects of past human impacts are known to be important for both ecological and social systems, but have been poorly studied to date [35,36]. Remote-sensing analyses were based on a 22-year time series and provide information on changes in land use, forest extent, timing and frequency of forest degradation and age of regeneration (see the electronic supplementary material, table S2). These data provide the basis for validating remotely sensed indicators of ecological and land-use change with direct field observations (e.g. retention and loss of forest biodiversity, forest fires and land-mechanization).

3. Practical lessons and realities from the field

The acquisition of extensive and reliable knowledge about the Amazon is dependent on research networks that can

effectively exploit economies of scale in shared resources and technical expertise, recognize and make explicit interconnections and feedbacks among sub-disciplines, and increase the temporal and spatial scale of existing studies [22]. However, building effective multi-sector and interdisciplinary research programmes at large spatial scales remains one of the most difficult challenges facing sustainability science [37].

One of the greatest challenges of the RAS project has been developing and maintaining engagement with partners from multiple sectors, institutions, local governments, civil society organizations and farmer associations. More than half of the remaining forest in the Amazon lies within private land [25], and one of the novel aspects of RAS is the collection of data from complex landscapes with multiple owners that encompass a broad spectrum of culture, wealth and education. Establishing contact, building a minimum level of trust, and securing permissions from more than 200 private landowners across the 36 study catchments incurred significant costs in time and resources. This was especially difficult in areas with a legacy of conflict over deforestation and the exploitation of natural resources. Such 'transaction costs' are rarely factored into or supported by funders of major research programmes.

Despite the challenges, most landowners recognized the value of research in strengthening the evidence basis for what are otherwise largely rhetorical and highly politicized debates regarding the effects and drivers of land-use change. The diversity of institutional partners that make up RAS, including local organizations, and those directly concerned with agricultural development and local conservation initiatives, was critically important in building trust. While the establishment of meaningful partnerships with very different types of landowners (including some of the poorest and richest farmers in the study regions) was critical for the success of RAS, it was also important to avoid over-promising and over-committing on the benefits to individual land owners from project outcomes. Considerable care was taken to manage expectations by distinguishing clearly the purpose of research from rural development and agricultural extension, and presenting realistic timetables for project participation and the dissemination of results.

Maintaining a meaningful level of engagement with our network of local partners is critical to help maximize the relevance of our analyses of project data to local sustainability problems [23]. We are keenly aware that the difficulties inherent in giving adequate attention to the needs and problems facing

local communities can increase the chance of drawing inappropriate conservation and development recommendations from our work. We are wary of presenting and interpreting trade-offs too simply, and we acknowledge that simplified quantitative analyses and narratives that only take account of a limited set of attributes can obscure important dynamics and dimensions of value, often resulting in the marginalization of some interest groups [38]. Although commonplace in research projects such risks are rarely made explicit.

Within the RAS research network, we encountered many of the problems faced by other multidisciplinary projects, including the need to overcome differences in values, language and modes of thinking among disciplines [22,24]. There are no easy answers to such challenges, though we have found that co-location of researchers from different disciplines within the same field teams, use of a shared online management platform and group exercises (such as participation in conference symposia and writing this paper) have all helped promote constructive dialogue. RAS has its origins in three previously independent research projects that were amalgamated together with more partners and funding sources into a single initiative with shared goals, budget and management structure. While this historical trajectory led inevitably to a more complex funding and communication system, the resulting strong sense of ownership shared by many project members often led to a more open, interactive and democratic decision making process during project planning and execution.

Many of the greatest challenges in developing RAS arose from mundane problems of coordinating the collection, processing and analysis of data. There is a need for continual reassessment of the value and purpose of new measurements or additional samples, and the extent to which more data are necessary to address the priority questions. Cost-effectiveness in time and resources are often ignored in conservation research (e.g. in biodiversity surveys [34,39]), yet the effectiveness of research would be significantly improved if these considerations were consistently taken into account in project planning and development. We suggest that complex projects such as RAS establish 'stopping rules', both in the collection of more field samples and in cutting losses in areas where progress is slow or negligible. The marginal costs of more field data may appear to be little, but they must take account the costs of laboratory and analysis work, and the transaction costs of managing increasing project complexity.

4. Next steps: guiding improvements in land-use sustainability

Work to address our first two objectives is ongoing in many disciplines in RAS to assess and better understand the ecological and socioeconomic consequences of land-use and landscape changes, with synthesis analyses of trade-offs and scenarios scheduled from 2013. We hope that the outcomes from RAS can help guide improvements in land-use policy and management in several ways. At the simplest level, the quantification of deleterious trends in valued attributes (e.g. declines in forest biodiversity, ecosystem service production and socioeconomic values) and the identification of key stressors can both help to identify management priorities. A clearer understanding of spatial patterns of ecological and socioeconomic condition is fundamental for

understanding the appropriate locations, scale, starting conditions and potential constraints associated with any future changes in management actions [40]. Such basic information is still lacking for much of the Amazon region.

RAS datasets can help reconcile social–ecological objectives and reveal trade-offs between farming and conservation at multiple spatial scales by combining data on socioeconomic and ecological values. One prominent debate concerns the effectiveness of alternative approaches for attempting to balance conservation and agricultural activities through changes in agricultural productivity and farming techniques, often referred to as land-sparing versus land-sharing [41]. Understanding of this general problem is limited by a lack of data on the conservation value of areas of remaining native vegetation available for conservation investment that are in differing stages of degradation or regeneration, farm-scale differences in agricultural productivity and other socioeconomic variables related to human well-being and poverty, and landscape-scale influences on local ecological and socioeconomic properties. RAS data can make a potentially important contribution to the development of Reducing Emissions from Deforestation and Degradation (REDD+) initiatives [42], recognizing that we currently have a very poor understanding of the relative ecological and socioeconomic costs and benefits of alternative forest conservation policies (e.g. avoided deforestation versus avoided degradation and forest restoration activities) and the interaction between such policies and the agricultural sector [43].

Data and results from RAS ultimately aim to contribute towards more sustainable land-use systems in Amazonia in five overlapping areas, namely the development of: (i) best practice recommendations for sustainable intensification and responsible agriculture, particularly in the cattle-ranching sector; (ii) cost-effective approaches to achieving compliance with environmental legislation, especially in Brazilian Forest Law; (iii) strategies for investment in forest conservation and restoration through payment for ecosystem service schemes, and particularly carbon finance; (iv) strategies for promoting fire-free agriculture; and (v) municipal-level ecological–economic zoning processes. We seek to identify potential opportunities and motivations for more sustainable development strategies in eastern Amazonia and elsewhere by combining the quantitative foundation of our sustainability assessment with input from stakeholders and work in the political and social sciences [44].

We hope that our data will be helpful to assess how changes in management incentives or regulatory conditions will influence relative ecological and socioeconomic costs and benefits. However, we also recognize that win–win solutions are rare and often misleading. Given this, our work seeks to give explicit consideration to possible conflicts, compromises and synergies among multiple objectives, unexpected interactions and feedbacks, and the broader political and institutional context [45].

Ensuring that the work being undertaken by RAS goes beyond science and successfully bridges the science–policy divide is both extremely challenging and unpredictable. There are at least three areas where we hope that our approach can help to increase opportunities for informing development and conservation decision makers. First, our interdisciplinary, mesoscale and place-based research approach increases the likelihood that our results are relevant and applicable to regional problems. Second, we believe that to be most effective

the process of knowledge exchange should occur across a broad and diverse set of actors as possible. Here, the participation of such a large group of (mostly Brazilian) students and researchers on the one hand, with a large and diverse array of non-research partners and associates (including conservation organizations, farmers groups, government agencies and individual landowners) on the other has provided the basis for multiple ongoing dialogues about our research objectives and preliminary findings. Knowledge exchange should not be limited to high-level executive summaries for policy makers but must exploit opportunities for shared learning and dissemination of ideas at all levels. Last, we are developing an impact strategy that can help to target the presentation and discussion of key results through appropriate media to specific audiences and demands at local, regional and national levels.

Sustainability science needs to balance the often-conflicting timetables of research and policy processes. As scientists we strive to ensure the reliability, intellectual credit and independence of our work; a process that often requires a lot of time. However, to influence the policy process effectively, our experience is that the research process also needs to be able to respond to limited and often unpredictable opportunities for contributing to decisions on management and policy. Engaging in this process requires innovative methods for interacting with

different sectors and contributing not only to the delivery of policy-relevant research outputs as outlined in this paper, but also to broader efforts to build the capacity and understanding necessary to create a more sustainable development trajectory for the Amazon region. We hope that the work of RAS can make a small contribution towards this enormous challenge.

This paper is dedicated to the late Manoel Aviz do Nascimento ('Nego') whose assistance to all aspects of RAS work in Santarém was so invaluable. We are grateful to the following for financial support; Instituto Nacional de Ciência e Tecnologia—Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0), Empresa Brasileira de Pesquisa Agropecuária—Embrapa (SEG: 02.08.06.005.00 and 01.05.01.003.05), the UK government Darwin Initiative (17-023), The Nature Conservancy, Natural Environment Research Council (NERC) (NE/F01614X/1, NE/G000816/1, NE/F015356/2 and NE/1018123), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (477583/2009-1), the Fulbright Commission (RH), São Paulo Research Foundation (FAPESP) (2011/19108-0), Fundação de Amparo à Pesquisa do estado de Minas Gerais (FAPEMIG), and the Brazilian Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). R.M. and J.R.T. were supported by Australian Research Council grant DP120100797. We also thank the farmers and workers unions of Santarém, Belterra and Paragominas and all collaborating private landowners and local government officials for their support. We are grateful to Paulo Brando, Jamila Haider and two anonymous reviewers for suggestions to improve the manuscript. More information about RAS can be found at www.redeamazoniasustentavel.org.

References

- Rockstrom J *et al.* 2009 A safe operating space for humanity. *Nature* **461**, 472–475. (doi:10.1038/461472a)
- Foley JA *et al.* 2011 Solutions for a cultivated planet. *Nature* **478**, 337–342. (doi:10.1038/nature10452)
- Nkonya E, Karsenty A, Msangi S, Souza CM, Shah M, vom Braun J, Galford G, Park S. 2012 *Sustainable land use for the 21st century*. New York, NY: United Nations Department of Economic and Social Affairs. Department for Sustainable Development.
- FAO. 2011 *The State of Forests in the Amazon Basin, Congo Basin and Southeast Asia*. Rome, Italy: Food and Agriculture Organization of the United Nations.
- Hansen MC, Stehman SV, Potapov PV. 2010 Quantification of global gross forest cover loss. *Proc. Natl Acad. Sci. USA* **107**, 8650–8655. (doi:10.1073/pnas.0912668107)
- Lambin EF, Meyfroidt P. 2011 Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl Acad. Sci. USA* **108**, 3465–3472. (doi:10.1073/pnas.1100480108)
- Steffen W *et al.* 2011 The anthropocene: from global change to planetary stewardship. *AMBIO* **40**, 739–761. (doi:10.1007/s13280-011-0185-x)
- Godfray HCl *et al.* 2010 Food security: the challenge of feeding 9 billion people. *Science (New York N.Y.)* **327**, 812–818. (doi:10.1126/science.1185383)
- Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA. 2007 Climate change, deforestation and the fate of the Amazon. *Science (New York N.Y.)* **319**, 169–172. (doi:10.1126/science.1146961)
- Peres CA, Gardner TA, Barlow J, Jansen J, Michalski F, Lees AC, Vieira ICG, Moreira FMD, Feeley K. 2010 Biodiversity conservation in human-modified Amazonian forest landscapes. *Biol. Conserv.* **143**, 2314–2327. (doi:10.1016/j.biocon.2010.01.021)
- Davidson EA *et al.* 2012 The Amazon basin in transition. *Nature* **481**, 321–328. (doi:10.1038/nature10717)
- Gardner TA. In press. The Amazon in transition: the challenge of transforming the world's largest tropical forest biome into a sustainable social-ecological system. In *Addressing tipping points* (eds T O'Riordan, T Lenton, I Christie). Oxford, UK: Oxford University Press.
- Andersen L, Granger C, Reis E, Weinhold D, Wunder S. 2002 *The dynamics of deforestation and economic growth in the Brazilian Amazon*. Cambridge, UK: Cambridge University Press.
- Nepstad D *et al.* 2009 Environment: the end of deforestation in the Brazilian Amazon. *Science (New York N.Y.)* **326**, 1350–1351. (doi:10.1126/science.1182108)
- Nepstad DC, McGrath DG, Soares-Filho B. 2011 Systemic conservation, REDD, and the future of the Amazon Basin. *Conserv. Biol.* **25**, 1113–1116. (doi:10.1111/j.1523-1739.2011.01784.x)
- Hecht SB. 2011 From eco-catastrophe to zero deforestation? Interdisciplinary, politics, environmentalisms and reduced clearing in Amazonia. *Environ. Conserv.* **39**, 4–19. (doi:10.1017/S0376892911000452)
- Boyd E. In press. Managing global tipping points: exploring the adaptive cycle metaphor and institutional responses to climate shocks. In *Addressing tipping points* (eds T O'Riordan, T Lenton, I Christie). Oxford, UK: Oxford University Press.
- Brussaard L, Caron P, Campbell B, Lipper L, Mainka S, Rabbinge R, Babin D, Pulleman M. 2010 Reconciling biodiversity conservation and food security: scientific challenges for a new agriculture. *Curr. Opin. Environ. Sustainability* **2**, 34–42. (doi:10.1016/j.cosust.2010.03.007)
- Collins SL *et al.* 2011 An integrated conceptual framework for long-term social–ecological research. *Front. Ecol. Environ.* **9**, 351–357. (doi:10.1890/100068)
- Becker BL. 2011 *Amazônia: Geopolítica na virada do III milênio*. Rio de Janeiro, Brazil: Garamond.
- Keller M, Gash J, Dias PS, Bustamante M (eds) 2009 *Amazonia and global change: a synthesis of LBA research*. Washington: American Geophysical Union.
- Barlow J *et al.* 2010 Using learning networks to understand complex systems: a case study of biological, geophysical and social research in the Amazon. *Biol. Rev. Camb. Phil. Soc.* **86**, 457–474. (doi:10.1111/j.1469-185X.2010.00155.x)
- Lahsen M, Nobre CA. 2007 Challenges of connecting international science and local level sustainability efforts: the case of the large-scale biosphere–atmosphere experiment in Amazonia. *Environ. Sci. Policy* **10**, 62–74. (doi:10.1016/j.envsci.2006.10.005)
- Perz SG *et al.* 2010 Crossing boundaries for environmental science and management:

- combining interdisciplinary, interorganizational and international collaboration. *Environ. Conserv.* **37**, 419–431. (doi:10.1017/S0376892910000810)
25. Ferreira J, Pardini R, Metzger JP, Fonseca CR, Pompeu PS, Sparovek G, Louzada J. 2012 Towards environmentally sustainable agriculture in Brazil: challenges and opportunities for applied ecological research. *J. Appl. Ecol.* **49**, 535–541. (doi:10.1111/j.1365-2664.2012.02145.x)
 26. Toledo de PM, Vieira ICG, Câmara G, Nobre CA. 2007 Integrating environmental and social agendas: the experience of the Amazonian networks LBA and GEOMA. In *Communicating global change science to society* (eds H Tiessen, M Brklacich, G Breulmann, RSC Menezes), pp. 109–118. New York, NY: Island Press.
 27. Clark WC, Dickson NM. 2003 Sustainability science: the emerging research paradigm. *Proc. Natl Acad. Sci. USA*, **100**, 8059–8061. (doi:10.1073/pnas.1231333100)
 28. Carpenter SR *et al.* 2012 Program on ecosystem change and society: an international research strategy for integrated social–ecological systems. *Curr. Opin. Environ. Sustainability* **4**, 134–138. (doi:10.1016/j.cosust.2012.01.001)
 29. Kareiva P, Tallis H, Ricketts TH, Daily GC, Polasky S. 2011 *Natural capital: theory and practice of mapping ecosystem services*. Oxford, UK: Oxford University Press.
 30. Brondizio ES, Moran EF. 2012 Level-dependent deforestation trajectories in the Brazilian Amazon from 1970 to 2001. *Popul. Environ.* **34**, 69–85. (doi:10.1007/s11111-011-0159-8)
 31. McIntire EJB, Fajardo A. 2009 Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* **90**, 46–56. (doi:10.1890/07-2096.1)
 32. DeFries R, Herold M, Verchot L, Macedo MN, Shimabukuro Y. 2013 Export-oriented deforestation in Mato Grosso: harbinger or exception for other tropical forests? *Phil. Trans. R. Soc. B* **368**, 20120173. (doi:10.1098/rstb.2012.0173)
 33. VanWey LK, Spera S, de Sa R, Mahr D, Mustard JF. 2013 Socioeconomic development and agricultural intensification in Mato Grosso. *Phil. Trans. R. Soc. B* **368**, 20120168. (doi:10.1098/rstb.2012.0168)
 34. Gardner TA *et al.* 2008 The cost-effectiveness of biodiversity surveys in tropical forests. *Ecol. Lett.* **11**, 139–50. (doi:10.1111/j.1461-0248.2007.01133.x)
 35. Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, Sodhi NS. 2009 Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* **12**, 561–582. (doi:10.1111/j.1461-0248.2009.01294.x)
 36. Brondizio ES, Ostrom E, Young OR. 2009 Connectivity and the governance of multilevel social-ecological systems: the role of social capital. *Annu. Rev. Environ. Resour.* **34**, 253–278. (doi:10.1146/annurev.environ.020708.100707)
 37. Carpenter SR *et al.* 2009 Science for managing ecosystem services: beyond the millennium ecosystem assessment. *Proc. Natl Acad. Sci. USA* **106**, 1305–1312. (doi:10.1073/pnas.0808772106)
 38. Hirsch PD, Adams WM, Brosius JP, Zia A, Bariola N, Dammert JL. 2011 Acknowledging conservation trade-offs and embracing complexity. *Conserv. Biol.* **25**, 259–264. (doi:10.1111/j.1523-1739.2010.01608.x)
 39. Hughes RM, Peck D. 2008 Acquiring data for large aquatic resource surveys: the art of compromise among science, logistics, and reality. *J. North American Benthol. Soc.* **27**, 837–859. (doi:10.1899/08-028.1)
 40. Tschardt T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005 Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. *Ecol. Lett.* **8**, 857–874. (doi:10.1111/j.1461-0248.2005.00782.x)
 41. Phalan B, Balmford A, Green RE, Scharlemann JPW. 2011 Minimising the harm to biodiversity of producing more food globally. *Food Policy* **36**, S62–S71. (doi:10.1016/j.foodpol.2010.11.008)
 42. Angelsen A, Brockhaus M, Sunderlin WD, Verchot LV (eds) 2012 *Analysing REDD+ : challenges and choices*. CIFOR: Bogor, Indonesia.
 43. Beddington JR *et al.* 2013 What next for agriculture after Durban? *Science* **335**, 290–298. (doi:10.1126/science.1217941)
 44. Le Tourneau F-M, Marchand G, Greissing A, Nasuti S, Droulers M, Bursztyn M, Léna P, Dubreuil V. 2013 The DURAMAZ indicator system: a cross-disciplinary comparative tool for assessing ecological and social changes in the Amazon. *Phil. Trans. R. Soc. B* **368**, 20120475. (doi:10.1098/rstb.2012.0475)
 45. McShane TO *et al.* 2011 Hard choices: making trade-offs between biodiversity conservation and human well-being. *Biol. Conserv.* **144**, 966–972. (doi:10.1016/j.biocon.2010.04.038)