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MUDANÇAS TEMPORAIS NA PRECIPITAÇÃO AFETAM A COMPOSIÇÃO TAXONÔMICA E FUNCIONAL DE ASSEMBLEIAS DE PEIXES EM IGARAPÉS DA AMAZÔNIA CENTRAL

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Manaus, Amazonas
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“Se você se sente impotente e confuso diante da situação global, está no caminho certo. Processos globais são complicados demais para que uma única pessoa os compreenda.”

Trecho do livro 21 lições para o século 21 de Yuval Noah Harari

Resumo

Os efeitos das mudanças climáticas nas assembleias biológicas locais são pouco conhecidos. Na Bacia Amazônica, as mudanças no padrão de precipitação nas últimas décadas devem afetar a dinâmica hidrológica dos igarapés, que dependem fortemente do regime local de chuvas. Tais mudanças podem alterar as características limnológicas e estruturais dos riachos e, consequentemente, perturbar as assembleias locais de peixes. Apresentamos aqui resultados de quatro eventos de amostragens repetidas de assembleias de peixes de igarapés realizadas em um intervalo de 17 anos (2001-2018) para investigar a dinâmica da composição taxonômica e funcional dos peixes e as possíveis influências das mudanças locais no regime hidrológico. As amostragens de peixes e a mensuração das variáveis ambientais foram realizadas por meio de um protocolo padronizado. Mudanças temporais na composição taxonômica e funcional das assembleias de peixes entre os quatro eventos de amostragem foram avaliadas quanto à magnitude, direção e congruência das trajetórias ao longo do tempo. Ao longo das duas últimas décadas, a precipitação total anual aumentou e os dias de tempestades (com precipitação superior a 20 mm) foram mais frequentes. A composição taxonômica e funcional das assembleias locais de peixes mudou entre os quatro eventos de amostragem, e as diferenças foram mais fortes entre o primeiro (2001) e o último (2018) ano de amostragem. As alterações nas assembleias de peixes afetaram a abundância relativa de algumas das espécies mais abundantes e foram aparentemente mediadas por alterações na composição do substrato (ou seja, mudando de áreas predominantemente cobertas por bancos de liteira para áreas de areia). Mudanças funcionais foram associadas a características relacionadas à aquisição de alimentos, locomoção e uso do habitat, resultando em menores abundâncias relativas de espécies que ocupam habitats de águas abertas no canal principal do igarapé e maior abundância de espécies capazes de usar as poças laterais e áreas marginais. Estes resultados fornecem evidências de uma mudança direcional na composição das assembleias de peixes, resultante dos efeitos do aumento da precipitação e uma maior frequência de tempestades nas últimas décadas. Considerando o curto intervalo de tempo avaliado e a sutileza das mudanças climáticas analisadas neste estudo, esses achados podem ser considerados surpreendentes e apontam para a necessidade da manutenção de programas de pesquisa ecológica de longo prazo em regiões tropicais, que concentram grande parte da biodiversidade do planeta.

Abstract

The effects of climate changes in local assemblages are poorly known. In the Amazon basin, changes in the rainfall pattern in the last decades are expected to affect the hydrological dynamics of forest streams, which strongly depends on the local rainfall regime. Such changes may alter limnological and structural characteristics of the streams and, consequently, disturb local fish assemblages. Here we present results of four repeated surveys of stream fish assemblages conducted along a time interval of 17 years (2001-2018) to investigate the dynamics of fish taxonomic and functional composition and the possible influences of local hydrological regime changes. Fish samplings and environmental variables measurements were conducted with a standardized protocol. Temporal changes in the taxonomic and functional composition of fish assemblages among the four surveys were evaluated regarding its magnitude, direction and congruence of trajectories along time. Throughout the two last decades, the total annual rainfall increased, and stormy days (with rainfall greater than 20mm) were more frequent. The taxonomic and functional composition of local fish assemblages changed among the four surveys, and differences were stronger between the first (2010) and last (2018) surveys. Changes in fish assemblages affected the relative abundance of some of the most abundant species and were apparently mediated by alterations in the substrate composition (i.e. shifting from predominantly covered by litter banks to open sand). Functional changes were associated to traits related to food acquisition, locomotion and habitat use, resulting in lower relative abundances of species that occupy open water habitats in the stream channel and higher abundances of species able to use the lateral ponds and shallow marginal areas. These results provide evidence of a directional change in fish assemblage composition resulting from the effects of increased precipitation and a higher frequency of stormy days over the last decades. Considering the short time interval evaluated and the subtleness of the climatic changes analyzed in this study, these findings can be surprising and point out to the need for the maintenance of long-term ecological research programs in tropical regions, which concentrate most of the planet's biodiversity.

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Introdução geral

As mudanças globais no clima são atualmente consideradas uma das maiores ameaças para a perda de biodiversidade (Bellard et al. 2012). Devido a essas mudanças, eventos climáticos extremos estão ocorrendo em maior intensidade e frequência nas últimas décadas (Duff et al. 2015, Gloor et al. 2018). Os distúrbios extremos do clima podem exceder a capacidade de aclimatação dos organismos (Gutschick & BassiRad 2003), podendo levar ao declínio das abundâncias de certas populações (Marchand et al. 2006), ou à extinção de populações e, portanto, a mudanças na composição de espécies das assembleias (Thibault & Brown 2008), de acordo com as interações bióticas e abióticas em cada ambiente (Fox 2013).

Alterações no clima local são projetadas para as regiões de altas latitudes, dos sub trópicos e dos trópicos (Garcia et al. 2014). Mais da metade da área global situada em regiões tropicais irá enfrentar grandes mudanças em relação à variação interanual histórica do clima (Garcia et al. 2014). Diversos estudos têm mostrado que alterações rápidas e severas no clima têm afetado a composição, diversidade ou funcionalidade de assembleias biológicas (Post et al. 2009; Hinzman et al. 2005; Thomas & Lennon 1999; Quayle et al. 2002; Turner et al. 2014). Porém, na região Neotropical há ainda pouco entendimento sobre como alterações rápidas e severas no clima afetam as diversas assembleias biológicas (e.g. Anciães and Peterson 2006, Buermann et al. 2011 para aves; Carey and Alexander 2003; Donnelly and Crump 1998 para anfíbios; e Röpke et al. 2017 para peixes de água doce). O entendimento dos efeitos de mudanças climáticas sobre animais nos Neotrópicos ainda é bem pequeno quando comparado aos estudos de larga escala espacial e temporal disponíveis para comunidades vegetais (e.g. Condit et al. 1996, Feeley et al. 2011). As predições dos modelos matemáticos indicam que as mudanças climáticas em curso no planeta podem causar uma modificação no regime de precipitação, tanto em frequência quanto em intensidade (Duffy et al. 2015). Há uma tendência de alteração do regime de precipitação com o aumento das chuvas na região central da Amazônia (Marengo 2004).

O Bioma Amazônico apresenta a maior diversidade de ambientes aquáticos do mundo e alta diversidade funcional de peixes (Pimm et al. 2015; Touissant et al. 2016), mas pouco se sabe sobre as consequências das mudanças climáticas nas comunidades desses organismos. Em geral, os estudos desenvolvidos até o momento buscam entender quais mecanismos estruturam as assembleias de peixes em resposta a mudanças abióticas ao longo de um ciclo sazonal ou em curta escala temporal (Espírito-Santo et al. 2009; Fitzgerald et al. 2017; Freitas et al. 2013). No entanto, Röpke et al. (2017) recentemente mostraram que um evento de seca extrema causou mudanças na assembleia de peixes e que condições hidrológicas anormais afetaram a assembleia de peixes de uma área de várzea na Amazônia Central ao longo das últimas duas décadas (1999-2014). A Amazônia tem enfrentado uma série de eventos climáticos extremos de secas (1997, 2005, 2010 e 2015) e cheias (2009, 2012, 2013 e 2014) (Tomasella et al. 2013, Marengo and Espinoza 2015, Röpke et al. 2017). As assembleias de peixes podem apresentar variações na estruturação funcional ao longo das fases do ciclo hidrológico (Fitzgerald et al. 2017), mas na presença de eventos extremos, essa estrutura funcional pode ser alterada (Röpke et al. 2017). Porém, essa conclusão pode ser generalizada para outras assembleias de peixes, em outros ambientes aquáticos na Amazônia? Essa é uma questão que permanece aberta em riachos dado que não estão sob dependência do pulso de inundação.

O regime de precipitação é especialmente importante para os sistemas de riachos (igarapés) amazônicos, que respondem muito rapidamente ao regime de chuvas local (Walker and Franken, 1983). Durante o período chuvoso são formadas poças laterais nas margens, que disponibilizam habitats para colonização de grupos de peixes com características especializadas (Pazin et al. 2006; Espírito Santo et al. 2016). Por exemplo, *Pyrrhulina brevis* aparentemente tem a capacidade de perceber mudanças hidrológicas decorrentes da pluviosidade e ajustar o uso das poças laterais, evitando o seu aprisionamento durante o processo de diminuição e mesmo desaparecimento desses ambientes. O sistema de poças laterais aos igarapés é previsível ao longo do ciclo sazonal, mas pode ser alterado em decorrência de distúrbios climáticos, prejudicando o seu uso pelos peixes (Espírito Santo et al. 2017). Por serem ambientes aquáticos que apresentam dependência do regime hidrológico local (Espírito-Santo et al. 2009), os igarapés da Amazônia Central são um bom modelo para identificar potenciais mudanças ocorridas devido aos eventos climáticos extremos ao longo das últimas décadas.

Dadas as mudanças climáticas em curso (aumento na intensidade de chuvas locais, aumento de precipitação durante a estação chuvosa, secas extremas) e as expectativas teóricas de que estas mudanças afetem as comunidades bióticas, eu analisei assembleias de peixes de 26 igarapés localizados na Reserva Florestal Adolpho Ducke na Amazônia Central (Fig. 1) em quatro momentos ao longo de um intervalo de 17 anos (2001 - 2018) para determinar se houve alterações em sua estrutura taxonômica e funcional relacionadas às alterações climáticas. Testei a hipótese que as mudanças climáticas graduais e/ou a ocorrência de eventos climáticos extremos funcionam como um filtro ambiental, selecionando grupo(s) de espécies com características funcionais capazes de resistir às alterações estruturais na dinâmica hidrológica desses ecossistemas aquáticos. Espero que o aumento gradual na precipitação tenha ocasionado alterações na disponibilidade espacial e temporal de recursos, causando mudanças direcionadas na composição de espécies ao longo do tempo. Por outro lado, o aumento da frequência de eventos extremos de chuva pode ter causado aumentos na turbulência e desestruturação do substrato, dificultando a natação e capacidade da manutenção da posição espacial das espécies que ocupam a coluna d’água no canal principal dos igarapés. Eventos esporádicos devem ter efeitos passageiros nas assembleias, e aparentemente era isso o que vinha ocorrendo. Entretanto, com o aumento da frequência e intensidade desses eventos extremos, é possível que a capacidade das assembleias de retornar ao estado original (resiliência) tenha sido superada.

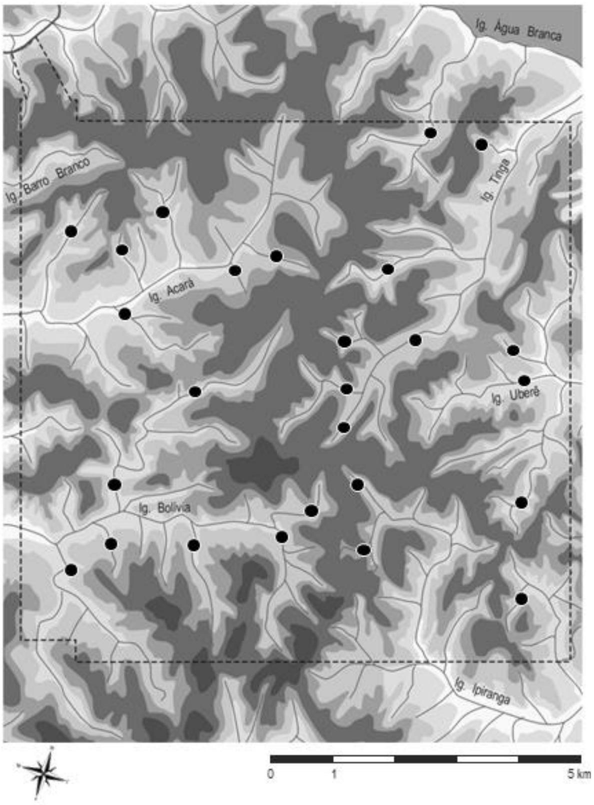

Figura 1. Mapa da área de estudo, Reserva Florestal Adolpho Ducke (RFAD) onde os pontos pretos indicam as parcelas aquáticas. A área em cinza demarca o platô central que divide a reserva em duas bacias de drenagem. Adaptado de Mendonça et al. (2005).

Objetivos

Objetivo geral

Determinar se a composição funcional das assembleias de peixes em igarapés na Amazônia Central vem sendo afetada por mudanças na pluviosidade local nas últimas décadas.

Objetivos específicos

- Identificar variações climáticas que poderiam afetar a assembleia de peixes em igarapés de terra firme na Amazônia Central no período de 2001 a 2018.
- Verificar se ocorrem mudanças na estrutura e nas características limnológicas dos igarapés em função de mudanças na pluviosidade observadas no período de 2001 a 2018.
- Avaliar se a estrutura funcional das assembleias de peixes de igarapés foi alterada entre os anos de 2001 e 2018.
- Determinar se existe relação entre variações na estrutura funcional das assembleias de peixes e mudanças na pluviosidade ocorridas entre os anos de 2001 e 2018.

Capítulo 1

Borba, G. C., et al. 2019.Temporal changes in rainfall affect taxonomic and functional composition of stream fish assemblages in central Amazonia. Manuscrito a ser submetido para o periódico *Ecography*

Temporal changes in rainfall affect taxonomic and functional composition of stream fish assemblages in central Amazonia

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Abstract

The effects of climate changes in local assemblages are poorly known. In the Amazon basin, changes in the rainfall pattern in the last decades are expected to affect the hydrological dynamics of forest streams, which strongly depends on the local rainfall regime. Such changes may alter limnological and structural characteristics of the streams and, consequently, disturb local fish assemblages. Here we present results of four repeated surveys of stream fish assemblages conducted over the last 17 years (2001-2018) to investigate the dynamics of fish taxonomic and functional composition and the possible influences of local hydrological regime changes. Fish samplings and environmental variables measurements were conducted with a standardized protocol. Temporal changes in the taxonomic and functional composition of fish assemblages among the four surveys were evaluated regarding its magnitude, direction and congruence of trajectories along time. Throughout the two last decades, the total annual rainfall increased, and stormy days (with rainfall greater than 20mm) were more frequent. The taxonomic and functional composition of local fish assemblages changed among the four surveys, and differences were stronger between the first (2001) and last (2018) surveys. Changes in fish assemblages affected the relative abundance of some of the most abundant species and were apparently mediated by alterations in the substrate composition (i.e. shifting from predominantly covered by litter banks to open sand). Functional changes were associated to traits related to food acquisition, locomotion and habitat use, resulting in lower relative abundances of species that occupy open water habitats in the stream channel and higher abundances of species able to use the lateral ponds and shallow marginal areas. These results provide evidence of a directional change in fish assemblage composition resulting from the effects of increased precipitation and a higher frequency of stormy days over the last decades. Considering the short time interval evaluated and the subtleness of the climatic changes analyzed in this study, these findings can be surprising and point out to the need for the maintenance of long-term ecological research programs in tropical regions, which concentrate most of the planet's biodiversity.

Keywords: ecological trajectory, functional composition, climate change, tropical freshwater, rainfall anomalies, temporal scale

Introduction

Global climate change is considered one of the main threats to biodiversity (Carpenter et al. 2011), and studies predict extinctions and/or dispersion of organisms to suitable climatic areas (Pearson et al. 2014, Urban 2015). Several studies showed that species tend to significantly alter their range, and local taxonomic composition for several animal groups (e.g., Miranda et al. 2019, Moritz et al. 2008). Studies on fish have shown effects mainly in their range distribution and population size (Baptista et al. 2015, Araújo et al. 2018), however their response are largely based on species distribution modeling techniques (Buisson et al. 2013, Oberdorff et al. 2015), whereas there are few empirical studies using long-term data (Daufresne and Boët 2007, Matthews and Marsh-Matthews 2016), and even less in regions of high fish biodiversity (Röpke et al. 2017, Freitas et al. 2013). We overcome such limitations by evaluating changes in species composition due to climatic changes in the tropical Amazônia.

The Amazon region is a great biodiversity center; it has the largest taxonomic (Reis et al. 2016, Tedesco et al. 2017) and functional (Touissant et al. 2016) diversity of freshwater fish on Earth. There are evidences of several extreme droughts (1997, 2005, 2010 and 2015) and floods events (2009, 2012, 2013 and 2014), mainly in the last two decades (Gloor et al. 2015). The consequences of these hydrological changes to the Amazonian freshwater fishes are scarce. Studying a large Amazonian river, Röpke et al. (2017) found consistent and permanent changes in species composition even eight year after the extreme drought event (2005); moreover, they also found that periodic-small and primary consumer species increased in relative abundance through time after the disturbance. Understanding the effects of the extreme events in biological communities, mainly focusing on trait assemblage attributes, is crucial to forecasting responses due to climate change in freshwaters. However, these examples focus on major rivers and tributaries, and studies of climate change effects in the small tropical forest streams and its fish fauna are still lacking.

The Amazonian streams form a complex network of small channels draining large forested areas and constitute a large part of the fluvial ecosystem (Junk et al. 1989). They are strongly dependent on the rainfall regime, responding rapidly to the local precipitation (Pazin et al. 2006, Espírito-Santo et al., 2009, 2013). Many species from the mainstream channel disperse to the marginal ponds formed during the flood period, resulting in a seasonal change in fish species composition in these streams (Espírito-Santo et al. 2009). The occurrence of heavy rainfall and storms can affect both the mainstream channel and the ponds, modifying the stream structure (habitats), hence directly and indirectly affecting fish assemblages (Espírito-Santo et al. 2009, Espírito-Santo et al. 2013). The annual precipitation over the Amazon basin has increased in the last decades, and alterations in hydrological regime are expected, especially in the central Amazonia (Marengo 2004). Further, increased precipitation levels could affect the time that marginal ponds retain water and its permanence over the years. As there is a strict relationship between species in ponds and stream channel (e.g. Espírito-Santo et al. 2013), one could expect changes in stream fish assemblage linked to changes in precipitation levels. Thus, the expected increased intensity and frequency of storms resulting from the current climate change may have been changing the natural dynamics of small Amazonian *terra-firme* streams and its biota.

The ichthyofauna of Amazonian streams presents large functional specialization due to the combination of extremes traits, and a high proportion of rare species (Leitão et al. 2016, Rodrigues-Filho et al. 2018). The presence of several ecologically specialized species with lower endurance to disturbance could decrease the community's resilience (Clavel et al. 2011, Röpke et al. 2017). Although resilience dictates how fast the ecosystem returns to pre-disturbance conditions (Pimm 1984), it would depends strongly on the magnitude of the environmental disturbance and if functional species groups are responding to this disturbance in different ways (Moritz and Agudo 2013). The use of traits composition could facilitate extrapolation and comparison with other studies. Also, it considers the ecological function of the species in the assemblage and not just a taxonomic response.

Here, we investigated the temporal dynamics of the functional and taxonomic structure of Amazonian stream fish assemblages over the last 17 years (2001-2018) and its relationship with local hydrological regime changes. We asked (a) do the taxonomic and functional composition of the stream fish assemblages have changed in the last 17 years? (b) If so, are these changes in fish composition related to climate changes (i.e., increase in local rainfall and in the frequency of storms)? (c) Do these changes in fish assemblage composition have a directional trend that could point to differential effects on some functional traits? We hypothesized that a local increase in local precipitation and in the frequency of stormy days would act as an environmental filter, selecting the lebiasinids (organisms capable of resisting the structural and hydrological changes of the streams because of their ability to movement from mainstream to ponds). Moreover, the high frequency of storms could lead to changes in the water discharge, affecting characin species due to its station-holding and motility attributes, which would reflect in directional changes in the functional composition of fish assemblages through time.

Material and Methods

Study area

The Ducke Forest Reserve (RFD) comprises 10.000 ha of *terra-firme* (non-flooded) rainforest, located northwest of Manaus (Amazonas state, Brazil). The mean temperature is 26°C, the mean annual rainfall (1965-2018) is 2244 mm (± 686 mm), mostly concentrated in the rainy season (December-May (Tomasella et al. 2008), (the dry season: July-October (Marques Filho et al. 1981).

RFD is a Brazilian site of the Long-Term Ecological Research Program (LTER) and has 38 permanents plots distributed across first- to third- order streams (according to the Stralher classification). The western slope of the RFD drains to the Negro River, whereas the eastern slope drains to the Amazon River (Mendonça et al. 2005).

Environmental and fish sampling

We obtained the rainfall data set from the RFD Meteorological Station (recording since 1966), and estimated trends in annual rainfall for the whole available data set, including our sampling period (from 2001 to 2018). To identify episodes of heavy rainfall, we estimated the number of days with rain > 20mm (i.e., storm index) as established by (Espírito-Santo et al. 2010), and used it as a proxy to the amount of water necessary to overflow streams. We also calculated the rain anomaly index (normalized anomaly = (observed value – historical mean value) / standard deviation of the historical series) (Feldpausch et al. 2017) to analyze the frequency and intensity of the dry and rainy years.

We collected fish and environmental data in 26 stream plots (first and second order) distributed throughout the RFD in 2001, 2005, 2011 and 2018. Each sampling plot represent a single day assessment of environmental and fish assemblage, mainly in the rainy-dry season transition (May to August) to reduce the influence of the seasonality on the sampling and fish detection. The data from 2001, 2005, and 2011 are from previous surveys from our research group (Mendonça et al. 2005, Espiríto-Santo et al. 2009, Espiríto-Santo et. al 2013), whereas 2018 is a new sampling event (present study).

In each sampling event both the local fish assemblage and physical-chemical features of sites have been registered according the *Igarapes* project protocol (http://www.igarapes.bio.br/, Mendonça et al. 2005) based on a 50m-long stream section. Shortly, we measured the stream structural features (mean width, depth, and water velocity) once in four equidistant transects along stream section, and record substrate composition in nine equidistant points across the stream in each of the four transects. The relative substrate composition (%) is estimated based on the categories pebble/gravel (110 mm), sand (0.1-1 mm), clay (0.05-0.1 mm), trunk (diameter > 10 cm), litter (dead leaves), fine litter (fine particulate organic matter), roots (of riparian vegetation) or aquatic plants. We measure flow velocity (m/s) at mid-channel in the center of the water column (Global Water Flow Probe, FP111) and the chemical characteristics such as conductivity (µS/cm), pH, dissolved oxygen (mg/L) and temperature (ºC) with a Horiba® (model U-52).

Before fish collection, we blocked stream sections previous the survey with nets (5 mm mesh size) at the extremes of the 50-m long to prevent fish escaping, and two collectors over two hours actively sampled fish with seine and hand nets. We keep the fish alive in buckets with stream water and a portable aerator, identified species (following the RFD fish guide, Zuanon et al. 2015), counted individuals and released them back promptly in the same sampling site. Non-identified specimens were euthanized with a lethal dose of Eugenol, fixed in 10% formalin and stored in 70% ethanol for subsequent identification. Our procedure is in accordance with federal laws (IBAMA, SISBIO #10.199-1) and institutional committee for ethics in research with animals (INPA, #10/2018).

We obtained the fish functional characteristics from Leitão et al. (2017) dataset in the same region of our study. They have taken seventeen ecomorphological measures from 5 to 15 individuals of each species expressing aspects of food acquisition, locomotion and habitat use of fish. Several studies consider the measures good proxies for functional response of fish species (Ribeiro et al. 2006, Teresa and Casatti 2017, Leitão et al. 2017, 2018). We used the Community Weighted Means (CWM) of functional traits to describe the functional structure of each local fish assemblage at each moment in time, because it incorporates the relative abundance of each the species. CWM is defined as the mean value of functional trait in a community weighted by the relative abundance of the species (Lavorel et al. 2008, Leitão et al. 2018), and was calculated with the dbFD function from the package FD (Laliberté and Legendre 2010).

Data analysis

Environment

We used PCA to reduce the dimensionality of the substrate composition and for the stream structural characteristics. Water chemical properties (conductivity and pH) could not be used due to calibration problems across sampling periods. Previous work suggests major differences chemical properties between west-east and minor changes in pH and conductivity within both drainage (Mendonça et al. 2005); as we are comparing species composition of individual points over time, water chemical properties are of minor importance here. A MANOVA was applied over the two first PCA axes to test for differences in substrate and stream structure between sampling periods. We tested differences in temperature and dissolved oxygen between periods with ANOVAs.

Fish species composition

We used Principal Coordinates Analysis (PCoA) to reduce dimensionality of species to observe changes in assemblage structure over time. For quantitative composition data (fish abundance), we adopted the Bray-Curtis dissimilarity index based on the species relative abundance in each site at each sampling period; we applied the Sørensen index for qualitative (presence-absence) data.

Functional trait

As our traits were all continuous, we used Principal Components Analysis (PCA) based on correlation to resume the functional information in two main dimensions. Each assembly was represented by a general CWM value to identify which traits most influenced the ordination in the functional dimensional space. From this two-dimensional representation we obtained the angles, by measuring the first and the last survey site position (Supplementary material Appendix 1, Fig.A1), to infer the direction of change in the assemblage sites over the total sampling period.

Taxonomic and functional composition

We tested for major differences in the taxonomic and functional composition over the sampling periods using Multivariate Analysis of Variance (MANOVA). We used the PCoA axes (derived from PCoA ordination) as response variables in Linear Mixed-effect Models (LMM), including the sampling sites as a random effect and the sampling period as a spatial autocorrelation term. Later, we used the LMM model results in a Tukey post-hoc test. We also evaluate changes in each site fish assemblage over the sampling period with paired t-tests. In this case, we compared differences in the ordination scores summarizing taxonomic and functional composition between the first (2001) and last (2018) sampling period. To check if the changes in sampling period differ between stream order over the sampling period, we repeated the paired t-test with each PCoA axes from the first to the last sampling period. Loadings of species and traits along the ordination axes were used to interpret the observed temporal changes.

We set an LMM to investigate if the magnitude of change in fish composition is related to the relationship between changes in fish composition and climatological changes (frequency of daily rain events greater than 20mm and rainfall variation registered in the interval of two subsequent sampling periods). The Euclidean distance between subsequent sampling periods in the two-dimensional ordination space were used as a dependent variable. Those were calculated from the PCoA scores of each site, from period t to period t+1. Sampling sites were included as a random effect, due to the replication across sampling periods. We included as covariates the stream size (stream order) and local conditions (water temperature, dissolved oxygen, substrate proportion). Finally, we used the angles obtained from the first and last survey position of each site to determine the direction of trajectory change on fish composition over the sampling periods. We used a linear model in this case, where the angles were the response variable and the stream order and substrate composition as covariates.

Espírito-Santo et al. (2009) observed that fish assemblage composition of the same streams presented a seasonal (cyclic) change. To test if the interannual changes observed in this study are significantly greater than the expected seasonal changes, we measured the changes in assemblage composition of each site (2005, dry season; 2006, rainy season; 2006, dry season) and compared with the overall interannual variation (2001 – 2018) using a paired t-test.

All analyses have been performed under R environment (The R Foundation for Statistical Computing) with vegan (Oksanen et al. 2017) , ape (Paradis and Schliep et al. 2019) , lme4, and multcomp (Hothorn et al. 2013) packages.

Results

Environmental trends

Total rainfall between 1966 and 2018, and the frequency of storms since 2005 increased through time (Fig.1a). From 2001 to 2018, there was a significant increment of anomalies (11 positive anomalies) and a high frequency of storm events (41 ± 13 storm days per year). In the 2001-2005 period, there was a single positive anomaly (2005) with the highest registered score in this period (2.12 index of the anomaly). Anomalies became more frequent and intense in the following years, we counted 11 positive and seven negative anomalies over the sampling period. Between 2005-2011 and 2011-2018, the frequency of storms increased 44 ± 6 and 35 ± 15 storm days per year, respectively (Supplementary material Appendix 1, Table A1, Fig.A2).

Substrate composition

We detected significant changes in substrate composition between sampling periods (MANOVA: Pillai-Trace= 0.406; F_4= 16.93; *P*-value= 0.001) that was similar across most local sites after 2005. Overall, the accumulated changes were from substrates predominantly covered by fine litter to sand-dominated substrates (Fig. 2d) (Supplementary material Appendix 1, Table A2). There was a significant temporal change in substrate composition both in first and second-order streams between 2001 and 2018. Both stream orders had consistent changes towards positive values of PC1, first-order (paired-t= 2.91, p-value=0.007, df= 16) and second-order streams (paired-t= 3.53, p-value= 0.007, df= 8) leading to a sandy substrate (Supplementary material Appendix 1 Fig. A3 (a)).

Temporal changes in the taxonomic structure of fish assemblages

The first two PCoA axes captured 49.2% (relative abundance data) and 58.4 % (presence/absence data) of variation in species composition, and only the former showed differences through time (Abundance, MANOVA: Pillai-Trace= 0.197; $F_{2.00}$= 12.4; p< 0.001) (Presence/Absence, MANOVA: Pillai-Trace= 0.038; $F_{2.00}$= 1.98; p= 0.14).

The relative abundance data showed a small and apparently non-directional change from 2001 to 2005 (Fig. 2e), but afterward the composition tended to show significant directional changes towards the lower right corner of the ordination space (Fig. 2f, g, h; 2001 – 2011:

p=0.03; 2001 – 2018: p<0.001; 2005 – 2018: p= 0.003). Considering the full-time interval, there was a significant change in species composition from 2001 to 2018, both along the first (paired-t=2.50, p= 0.01, df= 25) and the second PCoA axes (paired-t= -5.76, p< 0.001, df= 25) (Fig. 2h). The changes along the PCoA 1 was associated with increased relative abundances of the lebiasinid *Pyrrhulina* aff. *brevis* and the crenuchid *Microcharacidium eleotrioides*, and along PCoA 2 was associated mostly to an increase in the relative abundance of the crenuchid *Poecilocharax weitzmani* and decreasing abundances of the characins *Bryconops giacopinii*, *Hyphessobrycon* aff. *melazonatus* and *Iguanodectes geisleri* (Supplementary material Appendix 1, Table A3). Temporal changes also differed between stream orders (Supplementary material Appendix 1, Fig.A3(b)), with most sites in first order streams moving to the right along the PCoA axis1 (i.e., larger abundances of *P.* aff. *brevis* and *M. eleotrioides*, paired-t= 2.37, p= 0.03, df= 16), while most sites in second order streams moved towards negative values of second PCoA axes (i.e., larger abundances of *P. weitzmani*, paired-t= -4.19, p< 0.01, df= 8). The magnitude of change in fish composition was greater in second- compared to first- order streams. The LMM identified a significant relationship of the fish composition in abundance with the order stream (p= 0.007, adjusted R^2= 0.19).

There was also a significant temporal change in fish species composition based on presence/absence data from 2001 to 2018 along the PCoA1 (t= -2.40, p-value= 0.02, df= 25), but not along the PCoA 2 (t= 0.21, p-value= 0.83, df= 25). The ordination shows an overall directional composition change with site scores moving to the upper left corner of the multidimensional space along time (Fig. 2h). These changes were associated with a decreased frequency of occurrence of *Bryconops giacopinii*, *Iguanodectes geisleri*, *Hyphessobrycon* aff. *melazonatus*, *Hyphessobrycon agulha,* and an increased frequency of *Microcharacidium eleotrioides* and *Pyrrhulina* aff. *brevis* through time (Supplementary material Appendix 1, Table A4). The composition change differed among stream orders, with the first order streams showing a consistent change towards left along the PCoA 1 (t= 2.33, df= 16, p= 0.03) (Supplementary material Appendix 1, Fig. A3(c)). The interannual (among the 2001-2005-2011-2018 surveys) change in fish assemblage composition was significantly higher than the seasonal variation (2005 dry season – 2006 rainy season – 2006 dry season) observed for the same streams (t = -2.71, df = 24, p-value = 0.01).

Temporal changes in the functional structure of fish assemblages

There were significant changes in the functional structure of the fish assemblage between sampling periods when considering all sites (MANOVA: Pillai-Trace= 0.072; F_2= 3.96; p= 0.02). Comparing the full period (2001-2018), most sites moved towards the right side of the ordination space, but this change was marginally significant (t= 1.96, p-value= 0.06, df= 25) in the first axis (Fig.4). There was a decreasing of aspect ratio of pectoral fin (CPt), oral-gape shape (Osh), aspect ratio of the caudal fin (CFar) while pectoral-fin position (PFps) and number of teeth (Tnu) increased. It is indicating a selection of species with great maneuverability and able to feed on small food items. Along the second functional axis, there was a significant change (t= -3.06, p-value= 0.005, df= 25) associated with an increase of body transversal surface (Bsf; especially, in the last sampling periods, 2001-2011, p= 0.01; 2001-2018, p= 0.02) and a decreasing body mass (logM), indicating a predominance of fusiform-bodied species (Supplementary material Appendix 1, Table A5).

We also identified first-order streams changing significantly towards more positive values of the PCA axis 1 (t= 3.67, df= 16, p-value= 0.002), and second order streams tended to change in the opposite direction (Supplementary material Appendix 1, Fig.A3d). The LM based on the angles show temporal changes direction in stream order (p= 0.03, adjusted R^2= 0.16).

Discussion

Our study reveals an increase of total annual rainfall and a higher frequency of storms in the Ducke Forest Reserve during the last two decades. This regime shift modified the stream substrate composition from litter-dominated beds to a predominance of sand in stream bottom. Significant directional changes in the fish assemblage composition were also detected and an overall functional selection of species with good hydrodynamism and small body mass. Some of these changes were often linked to second-order streams, suggesting an interaction of local stream properties and the effects of precipitation changes. These directional changes after a time interval of only 17 years are surprising, given the supposed structural stability of forest streams in undisturbed landscapes (Espírito-Santo et al. 2009), and indicate that Amazonian stream fish assemblages may respond quickly to climate changes. This is the first time that consistent effects of climatic change on the taxonomic and functional structure are detected in tropical stream fish assemblages.

Amazonian climatic trends

The total rainfall precipitation over the Amazon basin increased in the last decades, and studies show an intensification of the hydrological cycle with stronger rainy seasons and more severe dry seasons (Gloor et al. 2015). The patterns documented here for RFD are in accordance with this trend. The increase in weather anomalies (extreme rain events) in the RFD area over the past two decades probably affected the hydrological regime of the *terra-firme* streams, with consequences for the local fish assemblages. Central Amazonia *terra-firme* streams are known to be dependent on the local rainfall regime, quickly responding to strong precipitation by overflowing the channel and washing the low relief marginal areas (Mendonça et al. 2005, Espírito-Santo et al. 2009). Increased flooding frequency is not expected to permanently change the physical structure of the stream channel but can affect the time that marginal ponds retain water and how many times the ponds are washed out by floods (e.g. Espírito-Santo et al. 2013). The dynamics of the substrate composition in the mainstream channel is thus likely to change with increased flooding frequency and intensity.

Changes in stream substrate composition

The directional changes in fish assemblages were apparently mediated by alterations in the substrate composition, which is a critical variable determining microhabitat use by stream fish (Pease et al. 2015, Ribeiro et al. 2016). Changes in substrate structure are consistently related to the intensification of rainfall and the occurrence of storms as headwaters respond rapidly to these intense events (Walker 1995). The complex substrates (mainly leaf litter banks and wood debris) tend to be washed out by the strong currents and increased water volumes (Espírito-Santo et al. 2009) and relocated in downstream reaches (Walker 1995), resulting in a structurally less-complex sandy substrate. The observed concomitant changes in substrate composition and fish assemblage structure with increasingly rainy and stormy years in the streams of RFD agree with these previous findings.

Temporal changes in fish assemblages

In agreement with our predictions, the increase in rainfall anomalies mediated by substrate alterations within streams indeed contributed to the compositional changes observed in stream fish communities as most changes was linked to the occurrence of more frequent storms (especially in 2005). As a result, abundant and generalist species like *Pyrrhulina* aff. *brevis* and

M. eleotrioides benefited and increased in relative abundance through time, probably due to their higher ability to deal with varying environmental conditions and the capacity of recolonization from adjacent systems. There was a concomitant decrease in frequency of occurrence and the relative abundance of pelagic species such as *B. giacopinii*, *I. geisleri*, *H.* aff. *melazonatus* and *H. agulha*, which are active swimmers, visually oriented species that occupy midwater and the water surface. The modified rainfall regime could have more strongly affected those pelagic species in several ways. They may have spent, for instance, more energy to maintain their position (i.e. station holding) at the stream water column, and/or their foraging efficiency presumably decrease in waters with high turbidity and turbulence (Winemiller et al. 2011), as is the case of Amazonian stream during the rainy season (Walker 1995, Espírito-Santo et al. 2009). These hypotheses, however, remain the be further experimentally evaluated.

The fish assemblage directional changes (i.e. relative abundance) were particularly evident over the years of stronger rainfalls and higher frequency of stormy days (e.g., 2005). The observed sensitivity of the studied fish assemblages in *terra-firme* streams to changes in rainfall regime points out to a low resilience face extreme climate events, contrary to the high resilience documented over 40 years of monitoring in USA streams (Matthews and Marsh-Matthews 2016). Resilience of fish assemblages in central Amazonia was thought to be high as there is evidence that a few years after a disturbance (such as reduced-impact logging) the fish fauna seem to return to its initial condition (Dias et al. 2010). Contrary to this previous study, the rainfall regime shift analyzed here are recurrent and our results are more consistent as the same sites have been compared through time (i.e., temporal controls). Even though stream fish exhibit high resilience in the short-term, a frequent and strong disturbance (such as the new rainfall regime) would promote divergence of assemblages over a large time scale (such as our; i.e., 17 years between initial and final conditions). Indeed, a recent study in the main Amazon river channel points to a low resistance and resilience of riverine fish assemblage after the 2005 drought (Ropke et al. 2017). Overall, our study suggests stream fish assemblages, even though protected by natural reserve areas, is sensitive to rainfall regime shifts and these effects can be detected in a few decades (i.e., 17 years).

Functional composition and fish traits selection related to rainfall changes

In Amazonian streams, species traits are associated with the instream conditions (i.e., habitat types, riparian cover). Most of these traits species are elongated bodies, rounded pectoral fins and relatively long head (Santos et al. 2019). The results obtained here indicate that the functional structure of the RFD fish communities is directionally changing, mainly related to the general body shape of species. Our data suggest small-bodied species (i.e., low body mass) and those with high transversal surface are being selected through time (overall a predominance of fusiform bodied species), which is compatible with an increase in maneuverability capacity (Sibbing and Nagelkerke 2000) under the new rainfall regime.

Our results indicate an increase in relative abundance of species with small-sized body and strong pectoral fins, indicating a higher ability to deal with varying microhabitat conditions in the streams. Intensification in rainfall regime can directly influence the flow discharge and the substrate restructuring, leading to alterations in streams dynamics. For instance, the traits selection related to locomotion and use of habitat inferred that species with elongated bodies and great maneuverability occurring in alluvial areas increase its frequency in overflow events in the streams. These traits contributed for lateral movements between channel and marginal ponds, benefiting species such as *Microcharacidium eleotrioides* and *Pyrrhulina* aff. *brevis* (Couto et al. 2017). *P.* aff. *brevis* occupies the upper layer of the water column in slow-flowing stretches in central Amazonia forest streams (Mendonça et al. 2005) and temporary lateral ponds during the flooding season periods (Pazin et al. 2006, Espírito-Santo et al. 2013, 2017). *M. eleotrioides* occurs in shallow and lateral complex environments (Mendonça et al. 2005, Pazin et al. 2006, Zuanon et al. 2015, Espírito-Santo et al. 2013). Both species are indeed abundant in ponds (Pazin et al. 2006), especially during the raining season (Espírito-Santo et al. 2013).

Because of its high functional diversity (Toussaint et al. 2016) and high functional redundancy (Leitão et al. 2017), Neotropical freshwater fish have been considered as less vulnerable compared to temperate ones. However, our results indicate that the functional space of Amazonian streams fishes is changing ongoing climatic temporal changes, despite having high functional diversity (Toussaint et al. 2016). This challenge the forecasted resilience of aquatic systems based solely on functional properties of its fish assemblages and points out to the need of long-term monitoring to understand the ecological meaning of such changes and its causes. The vulnerability of Amazonian stream fauna may be related to the historical high climatic and environmental stability of the Amazon basin (Peres et al. 2010, Rodrigues-Filho et al. 2018), which could impair its ability to cope with the quick and increasing disturbances resulting from current climatic changes.

Chain-Guadarrama et al. (2018) modeled CWM traits values to potential functional composition changes in a rain forest in Costa Rica under the projected climate changes (current and future). They identified that precipitation was a better CWM predictor than temperature. The traits selection suggested a shift from more conservative to more acquisitive tree species, which are more tolerant under climate changes. The lowland forest converged to on single direction with fast nutrient acquisition and fast growth species. As we saw in the present study, species tend to have a directional and a great magnitude of change against climate changes. The study founded evidences of changes with more than 57% of the study area showed changes in the CWM traits. This corroborated with our results, where there is a filtering selection of species with traits more tolerant to the ongoing climate changes.

Conclusion

We provided evidences that fish assemblages in *terra-firme* streams of central Amazonia show directional change in taxonomic and functional structure changes, mediated by alterations in substrate composition resulting from changes in rainfall dynamics over the last two decades. These forest streams have been considered stable environments, both today and in the past, and thus were not expected to be changing so fast with climatic change as observed here. The sensitivity of the *terra-firme* streams to climatic changes probably derives from their strong dependence on the local rainfall regime, which has been clearly changing in these last decades. However, more studies are necessary to disentangle the roles of short-, medium-, and long-term environmental changes on the stream fish assemblages, specially, in main relation between channel and lateral ponds. The subtleness of some observed changes in the taxonomic and functional structure of the fish communities points out to the question: are the observed changes in Amazonian streams going to turn to a premature “new normal” (Hobbs et al. 2006, (Matthews and Marsh-Matthews 2016)? The present study also evidences the importance of long-term datasets in ecology to detect possible changes in the structure and dynamics of ecological communities. Similarly, the functional approach employed in this study stands out as a promising tool to identify the more vulnerable species and help interpreting the ecological meaning of such changes in fish assemblages.

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Conclusões

As mudanças em curso no clima apontam para distúrbios extremos no regime hidrológico nos diferentes ecossistemas da Terra. Tais mudanças vêm resultando em reduções e reestruturações na dinâmica de comunidades de peixes. Isso pode estar relacionado a diferenças na resiliência das espécies.

No presente estudo pudemos detectar que o aumento da precipitação anual total e uma maior frequência de tempestades na RFD nas duas últimas décadas, teve uma correlação significativa entre essas mudanças hidrológicas e mudanças na composição do substrato, com uma mudança de substrato dominado por liteiras para uma predominância de areia. Houve uma seleção de características na direção de espécies generalistas com alta manobrabilidade e corpos pequenos. Algumas das mudanças diferiram entre as ordens de tamanho, sugerindo uma interação das propriedades locais dos igarapés com as mudanças climáticas. Essas mudanças direcionais ao longo de apenas 17 anos são surpreendentes, dada a estabilidade geral associada aos riachos da floresta em paisagens não perturbadas (Espírito-Santo et al. 2009), e indicam que as assembléias de peixes da Amazônia podem responder rapidamente às mudanças climáticas. Até onde sabemos, esta é a primeira vez que os efeitos da mudança climática nas comunidades de peixes tropicais são detectados.

Com isso, também fica evidente a importância de conjuntos de dados ecológicos de longo prazo para detectar possíveis mudanças na estrutura e dinâmica de comunidades ecológicas. Da mesma forma, a abordagem funcional utilizada neste estudo destaca-se como uma ferramenta promissora para detectar mudanças na estrutura das comunidades de peixes e para identificar as espécies mais vulneráveis às mudanças ambientais.

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Legends for figures

Figure 1. Temporal trends in precipitation at Ducke Forest Reserve from 1965 to 2018 (red vertical lines indicate survey years: 2001, 2005, 2011 and 2018). A) annual precipitation (dashed line shows linear regression, 6.08 ± 2.98 mm y^{-1}, 95% percent of confidence); B) frequency of stormy days (with precipitation higher than 20mm, following Espírito-Santo et al. 2011), where horizontal lines indicate mean ± 1 standard deviation.

Figure 2. Changes in substrate composition ordination at 26 stream sites along the time interval that include the surveys (2001, blue dots; 2005, red dots; 2011, green dots; 2018, black dots). Substrate categories with higher loadings on PC1 are shown below the graphs.

Figure 3. Trajectories of changes in the taxonomic composition of stream fish assemblages (species abundances) in four surveys conducted between 2001 and 2018. a) from 2001 (blue dots) to 2005 (red dots); b) from 2005 (red dots) to 2011 (green dots); c) from 2011 (green dots) to 2018 (black dots); d) overall trajectory from 2001 to 2018.

Figure 4. Trajectories of changes in the taxonomic composition of stream fish assemblages (species presence/absence) in four surveys conducted between 2001 and 2018. a) from 2001 (blue dots) to 2005 (red dots); b) from 2005 (red dots) to 2011 (green dots); c) from 2011 (green dots) to 2018 (black dots); d) overall trajectory from 2001 to 2018.

Figure 5. Trajectories of changes in the functional composition of stream fish assemblages in four surveys conducted between 2001 and 2018. a) from 2001 (blue dots) to 2005 (red dots); b) from 2005 (red dots) to 2011 (green dots); c) from 2011 (green dots) to 2018 (black dots); d) overall trajectory from 2001 to 2018. Functional traits with higher loadings on PC2 are shown below the graphs.

Figure 1.

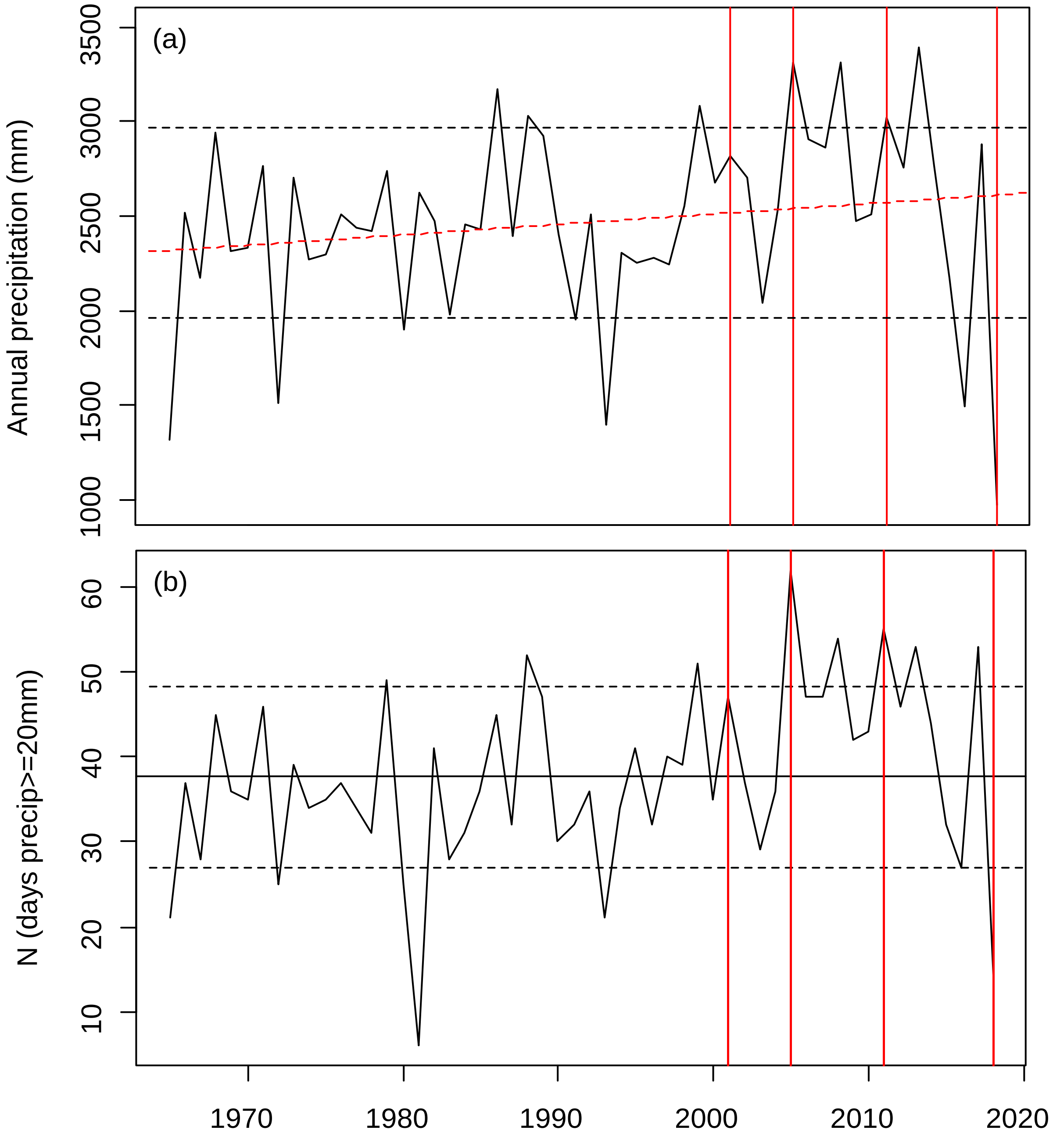

(a)
Annual precipitation (mm)
1000
1500
2000
2500
3000
3500
(b)
N (days precip>=20mm)
10
20
30
40
50
60
1970
1980
1990
2000
2010
2020

Figure 2.

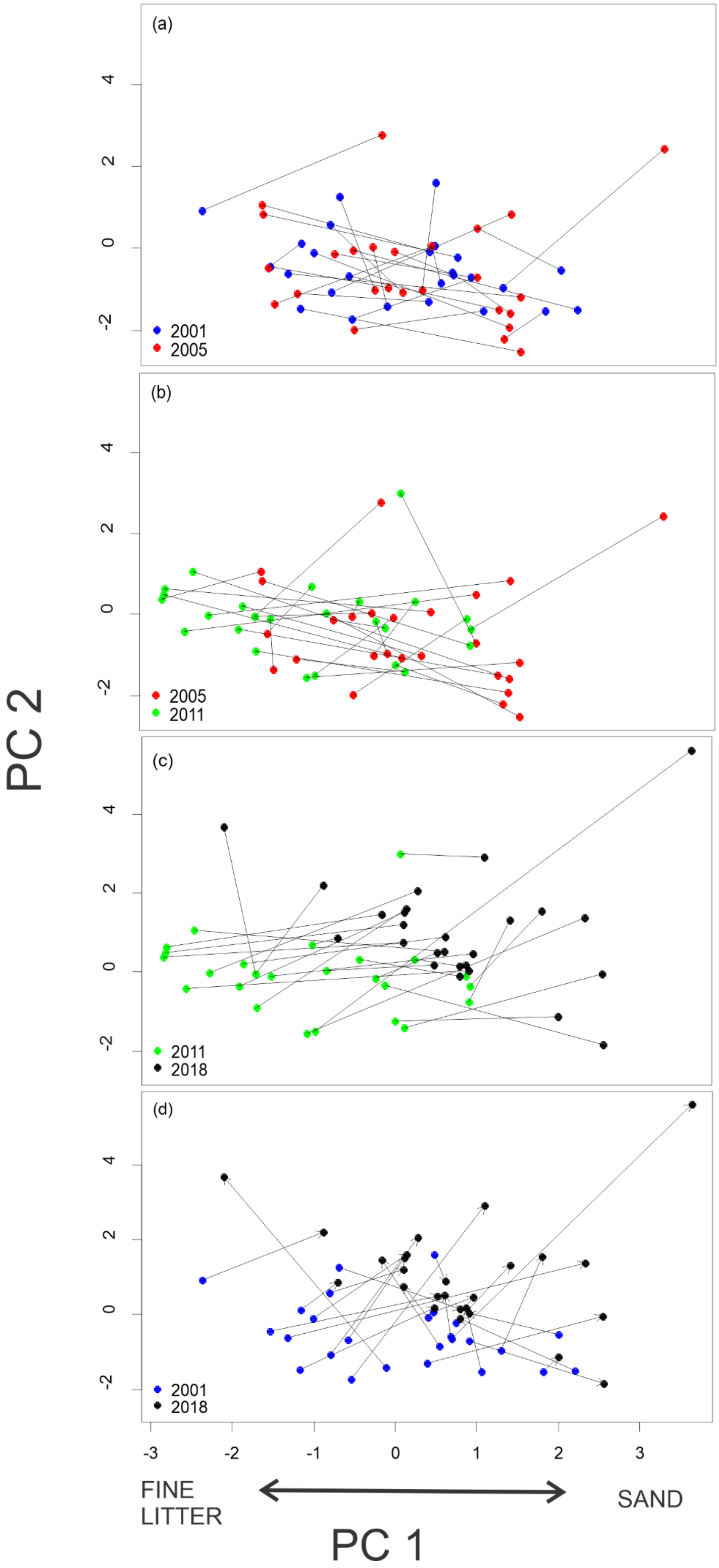

(a)
2001
2005
(b)
2005
2011
(c)
2011
2018
(d)
2001
2018
4
2
0
-2
-3
-2
-1
0
1
2
3
PC 2
FINE LITTER
SAND
PC 1

Figure 3.

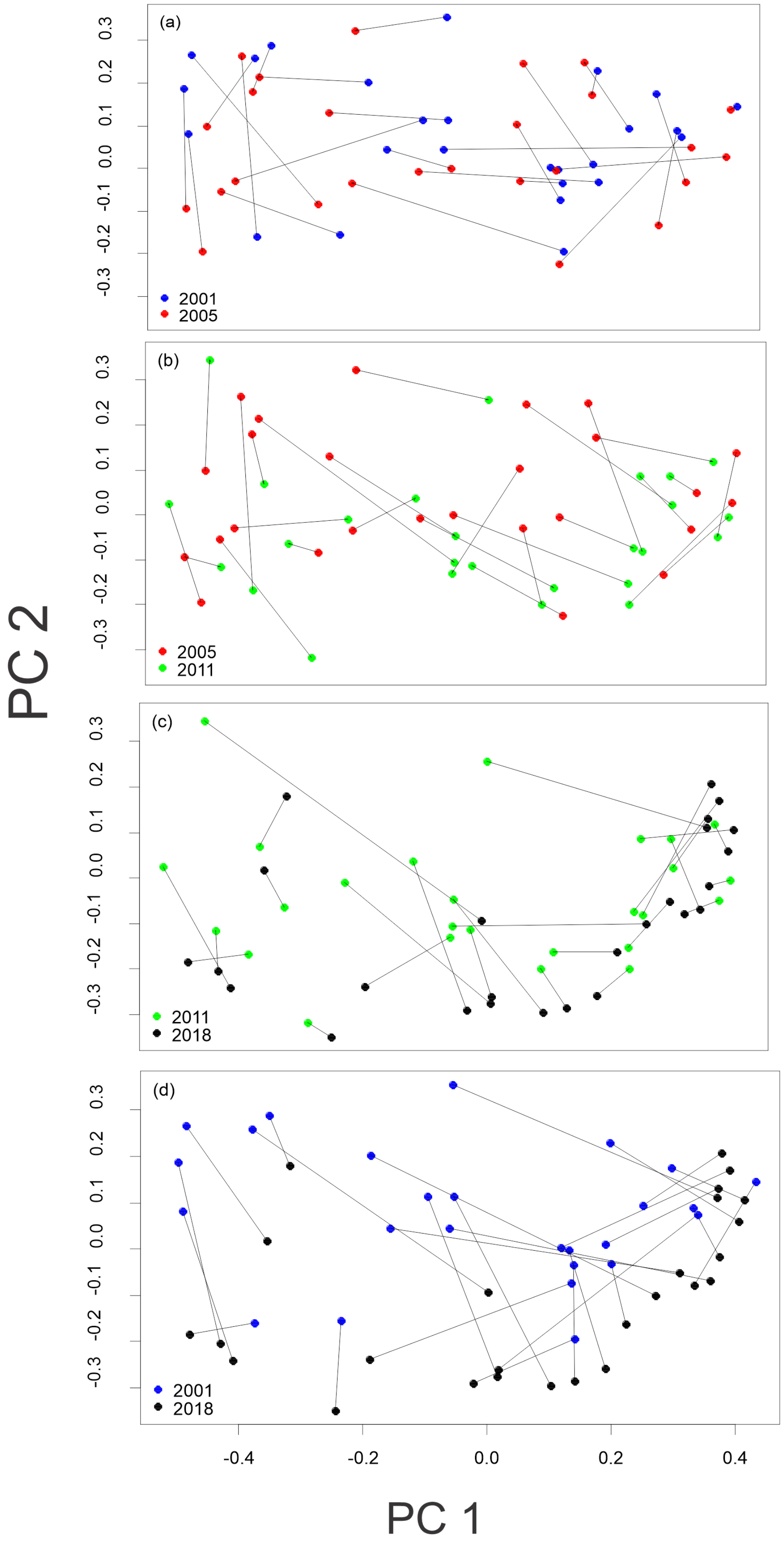

(a)
2001
2005
(b)
2005
2011
(c)
2011
2018
(d)
2001
2018
PC 2
PC 1
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
-0.4
-0.2
0.0
0.2
0.4

Figure 4.

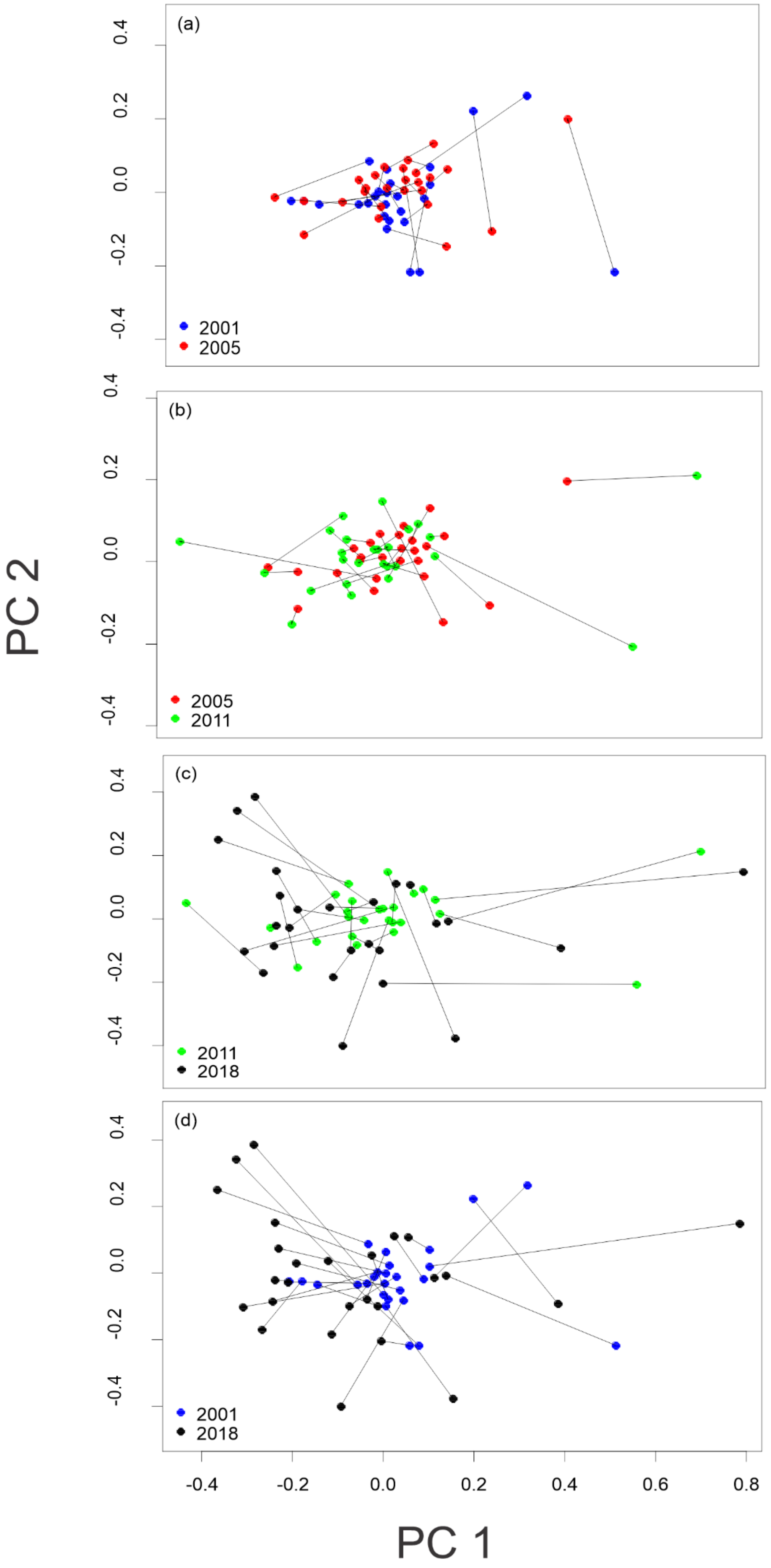
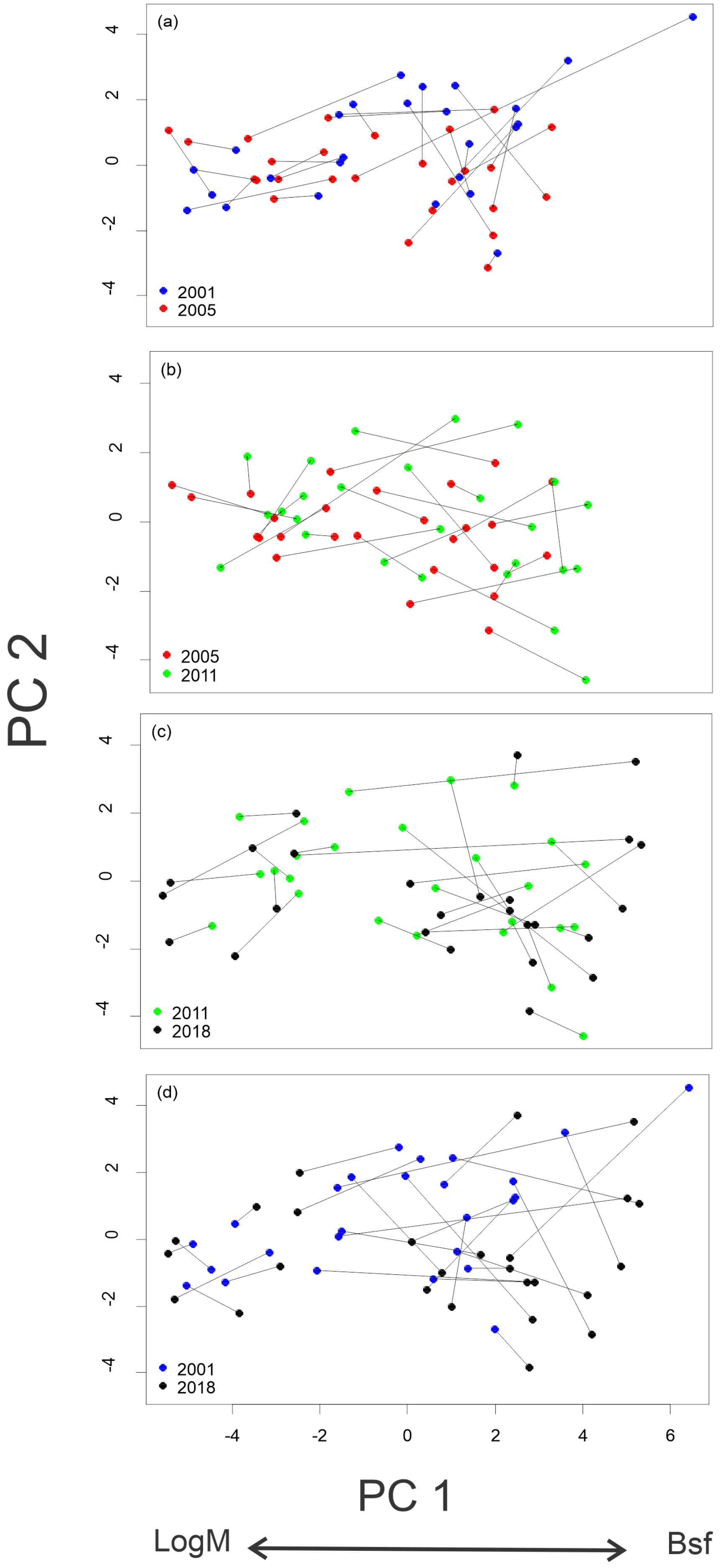

(a)
2001
2005
(b)
2005
2011
(c)
2011
2018
(d)
2001
2018
0.4
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
PC 2
PC 1

Figure 5.


(a)
2001
2005
(b)
2005
2011
(c)
2011
2018
(d)
2001
2018
4
2
0
-2
-4
PC 2
-4
-2
0
2
4
6
PC 1
LogM
Bsf

SUPPORTING MATERIAL

APPENDIX A

Temporal changes in rainfall affect the taxonomic and functional composition of stream fish assemblages in central Amazon

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Appendix A

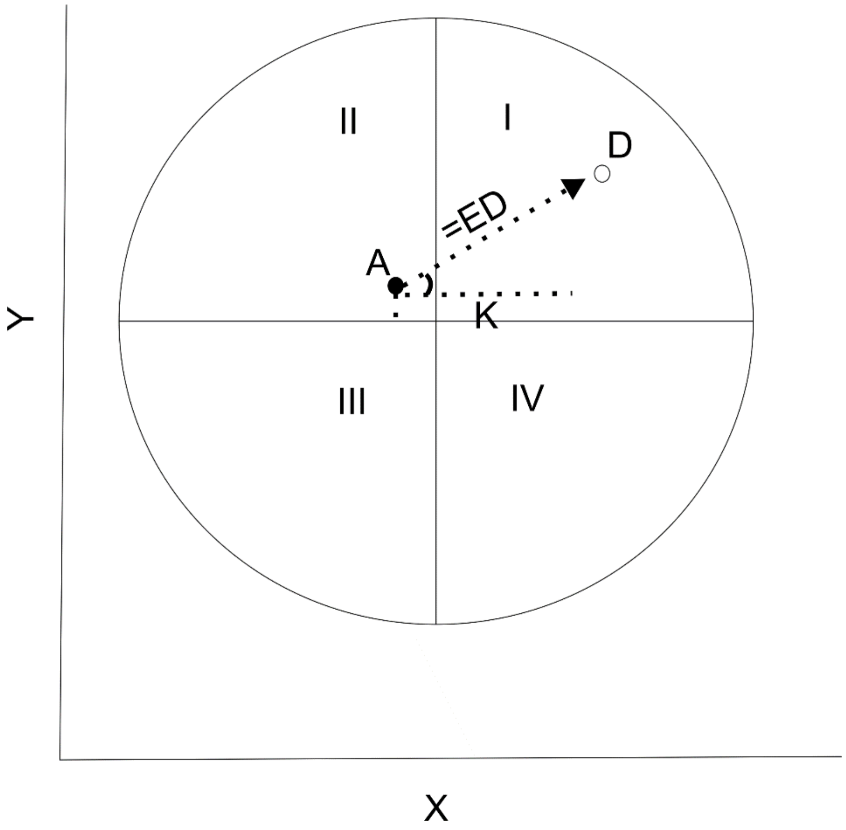

FIG.A1. Schematic representation of the calculation of the trajectory's angles of change in fish assemblage composition. The Euclidean distance (ED) from the initial (A) to final point position (D) in the multidimensional space. K is the difference between Y_D - Y_A.

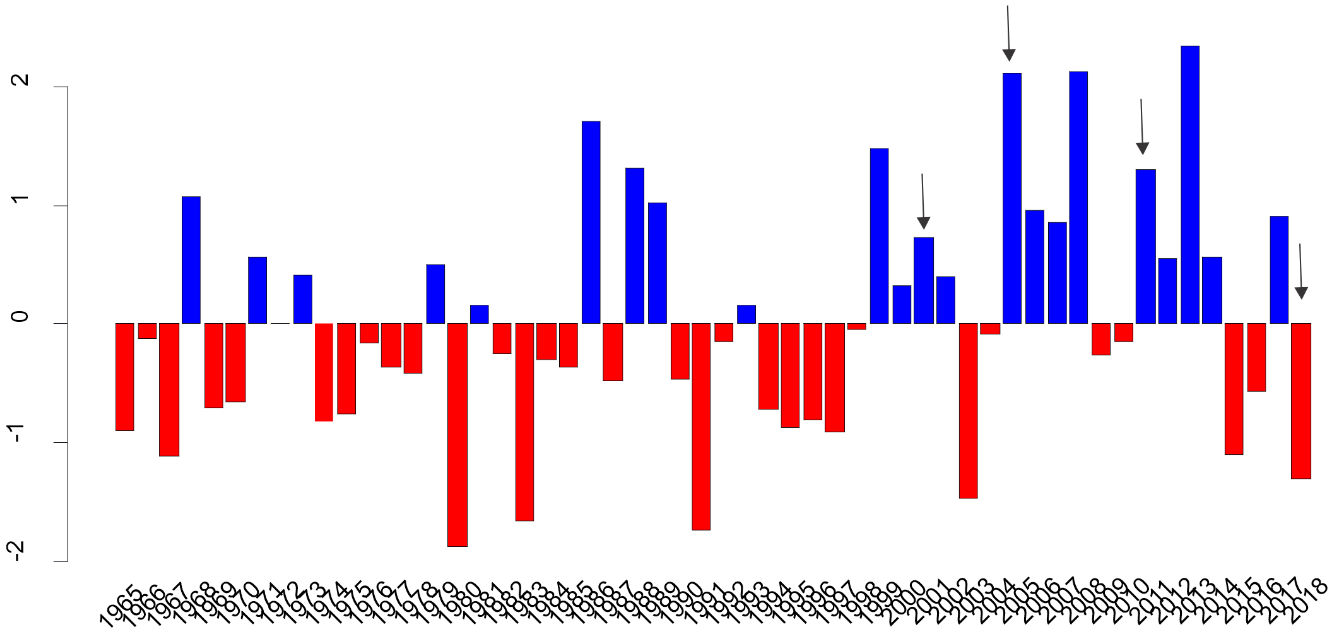

FIG.A2. Anomaly index for the historical rainfall (1965 – 2018) of Ducke Reserve (red bars, negative anomalies; blue bars, positive anomalies). Arrows indicate the survey periods (2001, 2005, 2011, 2018).

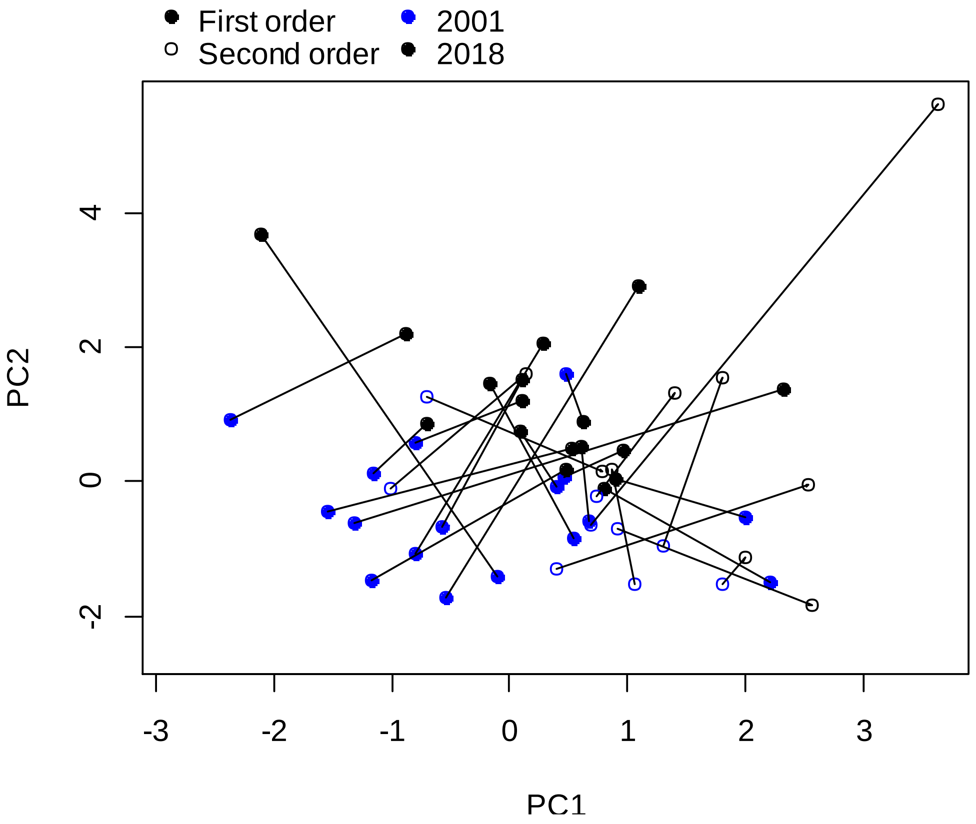

FIG. A3. Trajectory of changes in the substrate composition of 26 sampling sites from the first survey (blue symbols, 2001) to last survey (black symbols, 2018). Filled circles = first order stream; empty circles = second order streams.

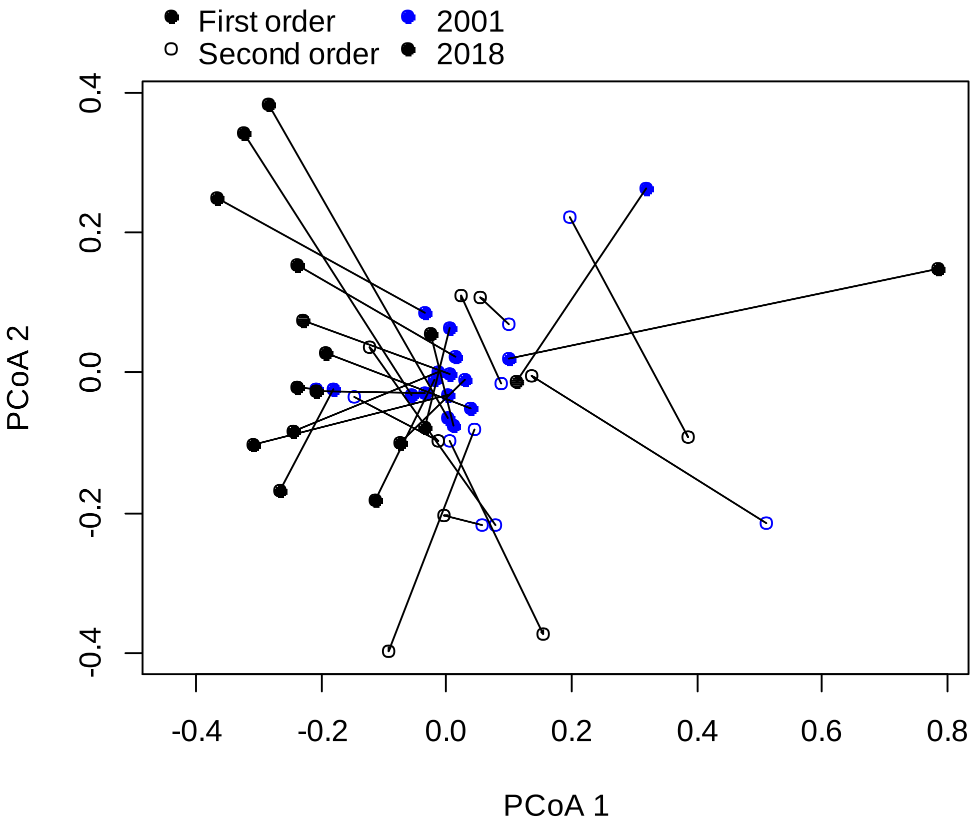

FIG.A5. Trajectory of changes in the fish assemblages abundance composition at 26 sampling sites from the first survey (blue symbols, 2001) to last survey (black symbols, 2018). Filled circles = first order stream; empty circles = second order streams.

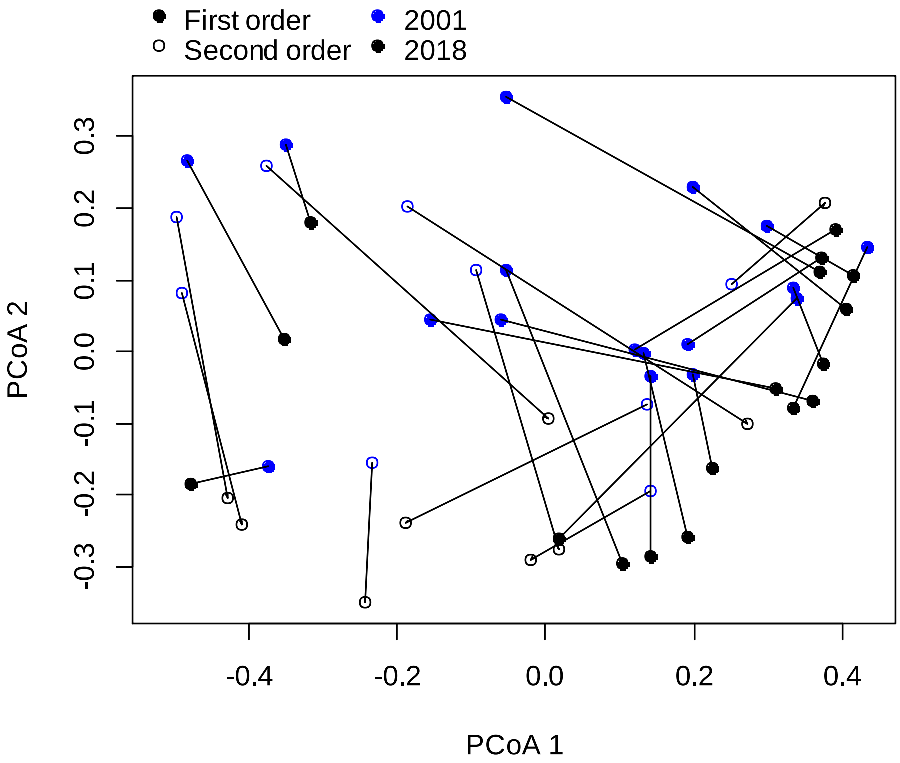

FIG. A4. Trajectory of the changes in the fish assemblages presence/absence composition at 26 sampling sites from the first survey (blue dots, 2001) to last survey (black dots, 2018). Filled circles = first order stream; empty circles = second order streams.

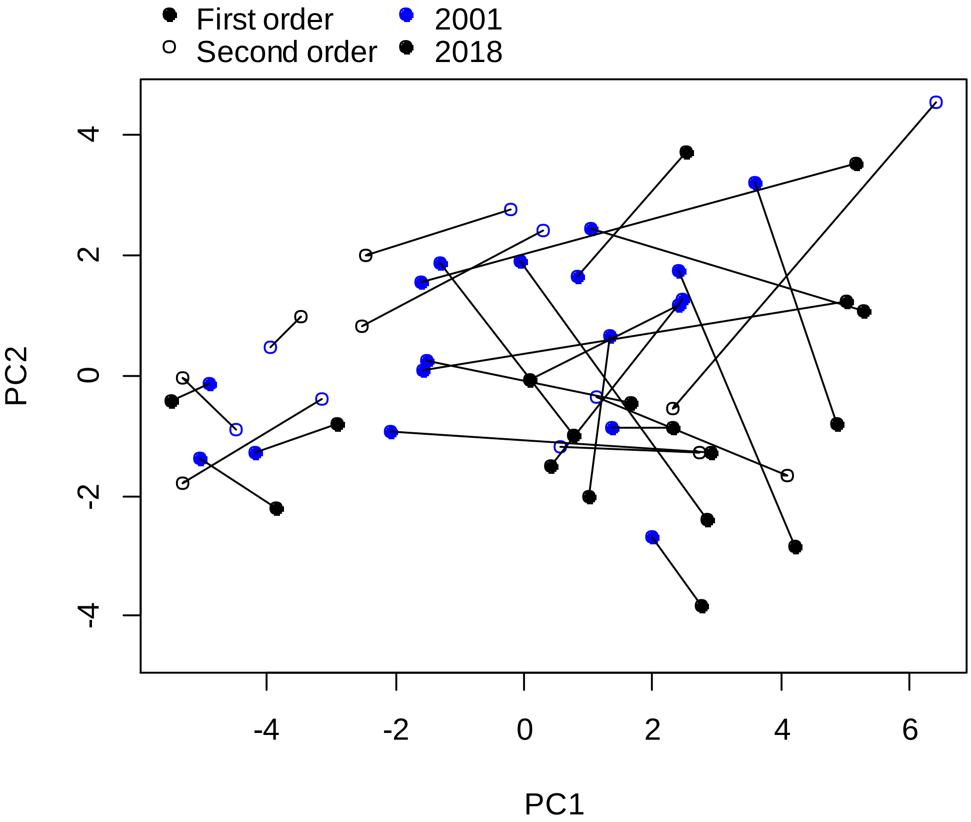

FIG. A6. Trajectory of the changes in the fish assemblages functional composition at 26 sampling sites from the first survey (blue symbols, 2001) to last survey (black symbols, 2018). Filled circles = first order stream; empty circles = second order streams.

Table A1. Values of total rainfall in the time interval between surveys.

Total Rainfall (mm)	**2001 - 2005**	**2005 - 2011**	**2011-2018**
Mean	1,971	2,592	2,187
Sd	± 678	± 475	± 910
Min	1,129	1,902	925
Max	2,703	3,312	3,387
rainy days > 20 mm	145	309	287

Table A2. Loadings of substrate proportion values of the fourth PC axes.

Variables	**PC1**	**PC2**	**PC3**	**PC4**
Sand	**0.758**	-0.566	0.154	0.100
Fine litter	**-0.643**	-0.204	-0.104	-0.412
Litter	**-0.637**	0.505	0.007	0.182
Aquatic herbaceous	0.205	0.588	-0.495	0.007
Fine roots	0.059	0.438	0.735	-0.075
Roots	-0.303	-0.505	-0.492	0.142
Cobble	0.149	0.364	-0.069	0.665

Trunk	0.465	0.344	-0.561	-0.21
Others	0.318	0.335	0.005	-0.564
Explained variance %	20.80	19.69	15.35	11.58
Accumulated variance %	20.80	40.50	55.85	67.43

Table A3. Loadings of abundance of the species in the first two PCoA axes.

Species	**PCoA 1**	**PCoA 2**
Aequidens_pallidus	0.003243	-0.15648
Ammocryptocharax_elegans	-0.21893	0.127819
Anablepsoides_micropus	0.226205	-0.07951
*Ancistrus*_aff._*hoplogenys*	-0.11881	-0.0291
Apistogramma_hippolytae	-0.03297	-0.10494
Batrochoglanis_raninus	0.003764	0.153102
*Bryconops*_cf._*caudomaculatus*	-0.09516	-0.11264
Bryconops_giacopinii	**-0.53036**	-0.32176
Bryconops_inpai	-0.16038	-0.12073
Callichthys_callichthys	-0.01397	0.079288
Carnegiella_strigata	-0.20196	0.212748
Characidium_pteroides	-0.1717	0.015696
*Crenicichla*_cf._*alta*	-0.09318	-0.19062
Crenicichla_inpa	-0.20035	-0.01772
Crenuchus_spilurus	-0.07716	-0.02647
Copella_nattereri	-0.07801	-0.04565
Denticetopsis_seducta	-0.1742	0.007135
Erythrinus_erythrinus	0.122902	0.227319
Gymnotus_coropinae	-0.16557	-0.17504
Gymnotus_pedanopterus	-0.35119	0.147139
*Gymnotus*_sp.._”TIG”	-0.01474	0.129932
Gymnotus_cataniapo	0.110529	-0.04637
Gymnorhamphichthys_rondoni	-0.13549	-0.14404
Gnathocharax_steindachneri	-0.00683	-0.17363
Hemigrammus_bellottii	-0.1717	0.015696
Helogenes_marmoratus	0.289475	0.041236
*Hemigrammus*_cf._*pretoensis*	0.337194	0.133573
Hoplias_malabaricus	-0.06763	0.029073
*Hyphessobrycon*_aff._*melazonatus*	**-0.63917**	0.50578
Hyphessobrycon_agulha	-0.15708	-0.05738
Hypopygus_lepturus	-0.33524	0.12525
Iguanodectes_geisleri	**-0.44487**	-0.15749
Imparfinis_pristos	-0.23344	0.015216
Ituglanis_ _amazonicus	-0.21155	-0.06764

Laimosemion_kirovskyi	0.307101	-0.12643
Mastiglanis_asopos	-0.15176	0.059978
Microcharacidium_eleotrioides	**0.411425**	-0.08465
Nannostomus_marginatus	-0.17051	-0.08945
*Nemuroglanis*_sp.	-0.23533	0.159598
Parotocinclus_longirostris	-0.29055	-0.11932
Phenacogaster_prolatus	-0.1247	0.15519
Poecilocharax_weitzmani	0.039366	**-0.22582**
Pygidianops_amphioxus	-0.18959	-0.08338
*Pyrrhulina*_aff._*brevis*	**0.549987**	0.397966
Rhamdia_quelen	-0.00423	0.142237
Rineloricaria_lanceolata	-0.18277	-0.03927
Steatogenys_duidae	-0.15584	0.067531
Sternopygus_macrurus	-0.11453	0.156158
*Synbranchus*_sp.	-0.02897	-0.04071

Table A4. Loadings of presence/absence values from the first two PCoA axes.

Species	**PCoA 1**	**PCoA 2**
Aequidens_pallidus	-0.04357	-0.15743
Ammocryptocharax_elegans	0.236283	-0.14944
Anablepsoides_micropus	-0.20446	0.038716
*Ancistrus*_aff_*hoplogenys*	0.136734	-0.24737
Apistogramma_hippolytae	0.128847	-0.08347
Batrochoglanis_raninus	-0.03179	-0.06503
*Bryconops*_cf_*caudomaculatus*	0.096384	-0.05897
Bryconops_giacopinii	**0.632398**	0.199583
Bryconops_inpai	0.17422	0.180065
Callichthys_callichthys	-0.09563	-0.0184
Carnegiella_strigata	0.237981	-0.0975
Characidium_pteroides	0.353559	0.173144
*Crenicichla*_cf_*alta*	0.031548	0.065267
Crenicichla_inpa	0.157286	0.293275
Crenuchus_spirulus	-0.00867	0.070768
Copella_nattereri	-0.01107	-0.1815
Denticetopsis_seducta	0.253481	0.208604
Erythrinus_erythrinus	-0.01175	0.119193
Gymnotus_coropinae	-0.09959	0.334434
Gymnotus_pedanopterus	0.239323	0.020455
*Gymnotus*_sp "TIG"	-0.04775	0.030573
Gymnotus_cataniapo	-0.13624	-0.13716
Gymnorhamphichthys_rondoni	0.070361	-0.00421
Gnathocharax_steindachneri	-0.00649	-0.07918

Hemigrammus_bellottii	0.353559	0.173144
Helogenes_marmoratus	-0.18066	0.517349
*Hemigrammus*_cf_*pretoensis*	-0.27729	-0.42736
Hoplias_malabaricus	-0.02454	0.049648
*Hyphessobrycon*_aff_*melazonatus*	**0.596401**	0.101931
Hyphessobrycon_agulha	**0.447025**	-0.20062
Hypopygus_lepturus	0.262567	-0.09342
Iguanodectes_geisleri	**0.541984**	0.198021
Imparfinis_pristos	0.35897	0.213657
Ituglanis amazonicus	0.236523	-0.12823
Laimosemion_kirovskyi	-0.38554	0.226232
Mastiglanis_asopos	0.052472	0.031912
Microcharacidium_eleotroides	**-0.487**	0.043619
Nannostomus_marginatus	0.01578	0.255264
*Nemuroglanis*_sp	0.259019	0.107801
Parotocinclus_longirostris	0.378712	0.132889
Phenacogaster_prolatus	0.029083	-0.17677
Poecilocharax_weitzmani	-0.16363	0.116027
Pygidianops_amphioxus	0.330227	0.265268
*Pyrrhulina*_aff_*brevis*	**-0.54281**	-0.11856
Rhamdia_quelen	-0.05471	-0.03411
Rineloricaria_lanceolata	0.240463	0.199869
Steatogenys_duidae	0.049206	-0.09808
Sternopygus_macrurus	0.141194	-0.12231
Synbranchus_sp	-0.13625	0.371838

Table A5. Loadings of each trait value in the first two RDF axes.

Traits	**PC1**	**PC2**
logM	-0.04008	**0.500771**
Osf	-0.27661	0.128047
Osh	-0.32557	0.018528
Ops	0.023101	-0.19376
Prt	0.217843	0.171216
Edst	-0.14271	**-0.36465**
Eps	0.224229	0.295911
Bsh	-0.1628	0.286473
Bsf	0.150582	**-0.37538**
PFps	0.301713	0.152471
PFar	-0.25174	-0.25655
CPt	-0.31535	0.090999
CFar	-0.32109	0.134441

Frt	0.279767	0.167419
Fsf	0.279557	-0.26167
Tnu	0.305869	-0.05338
Rsh	-0.20283	-0.08574

Table A6. List of the 17 functional traits measured for stream fishes from the Ducke Reserve.

Trait	Calculation/Class	Nature	Ecological meaning	References
Number of teeth (Tnu)	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 Intermediate Long/ numerous	Ordinal	Filtering ability and gill protection	adapted from Sibbing & Nagelkerke (2001)
Protrusion length (Prt)	$\frac{Prt}{Sn}$	Continuous	Nature of food items captured and feeding method	adapted from Gatz (1979)
Oral-gape surface (Osh)	$\frac{Mw \times Md}{Bw \times Bd}$	Continuous	Nature/Size of food items captured	adapted from Karpouzi & Stergiou (2003)
Oral – gape position (Ops)	$\frac{Mo}{Hd}$	Continuous	Feeding method in the water column	adapted from Sibbing & Nagelkerke (2001)
Eye size (Edst)	$\frac{Ed}{Hd}$	Continuous	Prey detection	adapted from Boyle & Horn (2006)
Eye position (Eps)	$\frac{Eh}{Hd}$	Continuous	Vertical position in the water column	Gatz (1979)

Body transversal shape (Bsh)	$\frac{Bd}{Bw}$	Continuous	Vertical position in the water column and hydrodynamism	Sibbing & Nagelkerke (2001)
Body transversal surface (Bsf)	$\frac{\ln\ [(\frac{\pi}{4} \times Bw\ \times Bd) + 1]}{\ln(\text{Mass} + 1)}$	Continuous	Mass distribution along the body for hydrodynamism	Villéger et al. (2010)
Pectoral-fin position (PFps)	$\frac{PFi}{PFb}$	Continuous	Pectoral fin use for maneuverability	Dumay et al. (2004)
Aspect ratio of the pectoral fin (FPar)	$\frac{PFl^2}{PFs}$	Continuous	Pectoral fin use for propulsion	adapted from Fulton et al. (2001)
Caudal fin – peduncle depth ratio (Cpt)	$\frac{CFd}{CPd}$	Continuous	Caudal propulsion efficiency through reduction of drag	Webb (1984)
Aspect ratio of the caudal fin (CFar)	$\frac{CFd^2}{CFs}$	Continuous	Caudal fin use for propulsion and/or direction	Webb (1984)
Fins surface ratio (Frt)	$\frac{2 \times PFs}{CFs}$	Continuous	Main type of propulsion between caudal and pectoral fins	Villéger et al. (2010)
Fins surface to body size ratio (Fsf)	$\frac{(2\ \times PFs) + CFs}{\frac{\pi}{4} \times Bw\ \times Bd}$	Continuous	Acceleration and/or maneuverability efficiency	Villéger et al. (2010)

Body mass (LogM)	log (Mass + 1)	Continuous	Metabolism, endurance and swimming ability	Villéger et al. (2010)

Table A7. List of fish species sampled in 26 streams of Ducke Reserve in the four surveys conducted between 2001 and 2018.

ORDER	**Survey period**			
Family				
Species	**2001**	**2005**	**2011**	**2018**
CHARACIFORMES				
Acestrorhynchidae				
Acestrorhyncus falcatus (Bloch, 1794)	2	1	0	0
Characidae				
Bryconops cf. *caudomaculatus*	0	0	20	8
Bryconops inpai Knöppel, Junk & Géry, 1968	35	38	43	18
Bryconops giacopinii (Fernández-Yépez, 1950)	65	289	163	144
Carnegiella strigata (Günther, 1964)	0	1	2	0
Gnathocharax steindachneri Fowler, 1913	0	0	0	2
Hemigrammus cf. *pretoensis*	166	102	85	33
Hyphessobrycon cf. *agulha*	39	24	17	58
Hyphessobrycon aff. *melazonatus* Durbin *in* Eigenmann, 1908	535	633	286	101
Iguanodectes geisleri Géry, 1970	23	24	28	59
Crenuchidae				
Ammocryptocharax elegans Weitzman & Kanazawa, 1976	0	6	2	0
Crenuchus spilurus (Günther, 1863)	31	53	34	31
Microcharacidium eleotrioides Géry, 1960	83	159	181	121
Poecilocharax weitzmani Géry, 1965	2	43	20	78
Erythrinidae				
Erythrinus erythrinus (Schneider, 1801)	98	35	19	7
Hoplias malabaricus (Bloch, 1794)	2	2	4	1
Lebiasinidae				
Copella nattereri (Steindachner, 1876)	11	29	8	14
Copella nigrofasciata (Meinken, 1952)	23	16	38	
Nannostomus marginatus Eigenmann, 1909	15	7	10	
Pyrrhulina aff. *brevis* Steindachner, 1876	388	333	331	206
CYPRINODONTIFORMES				
Rivulidae				
Anablepsoides micropus (Steindachner, 1863)	0	0	39	6

Laimoseminion kirovskyi (Costa, 2004)	0	0	100	41
GYMNOTIFORMES				
Gymnotidae				
Gymnotus cataniapo Mago-Leccia, 1994	0	0	0	2
Gymnotus coropinae Hoedeman, 1962	4	38	38	24
Gymnotus pedanopterus (Mago-Leccia, 1994)	6	10	3	3
Gymnotus sp. "TIG"	0	2	0	0
Hypopomidae				
Hypopygus lepturus (Hoedeman, 1962)	7	19	0	0
Microsternarchus bilineatus (Fernández-Yépez, 1968)	3	16	13	
Steatogenys duidae (La Monte, 1929)	2	3	0	0
Rhamphichthyidae				
Gymnorhamphychthys rondoni (Ribeiro & Miranda, 1920)	0	0	0	1
Sternopygidae				
Sternopygus macrurus	8	8	8	8
PERCIFORMES				
Cichlidae				
Aequidens pallidus (Heckel, 1840)	125	142	104	78
Apistogramma hippolytae Kullander, 1982	0	0	1	3
Crenicichla cf. *alta* Eigenmann, 1912 Millet	0	0	1	0
Crenicichla inpa Ploeg, 1991	2	2	1	1
SILURIFORMES				
Callichthyidae				
Callichthys callichthys (Linnaeus, 1758)	2	1	2	0
Cetopsidae				
Denticetopsis seducta Vari, Ferraris & de Pinna, 2005	0	0	2	0
Helogenes marmoratus (Günther, 1864)	36	38	36	23
Heptapteridae				
Imparfinis pristos Mees & Cala, 1989	0	3	6	0
Mastiglanis asopos Bockmann, 1994	0	6	0	0
Nemuroglanis sp.	0	5	15	0
Rhamdia quelen (Quoy & Gaimard, 1863)	1	1	0	0
Pseudopimelodidae				
Batrochoglanis raninus (Valenciennes, 1840)	0	0	1	0
Loricariidae				
Ancistrus aff. *hoplogenys* (Günther, 1864)	1	5	12	9
Parotocinclus longirostris Garavello, 1988	0	5	2	0
Rineloricaria lanceolata (Günther, 1868)	0	0	4	0
Trichomycteridae				
Ituglanis amazonicus (Steindachner, 1882)	1	0	0	1
Pygidianops amphioxus de Pinna & Kirovsky, 2011	0	4	5	0
SYNBRANCHIFORMES				
Synbranchidae				

Synbranchus sp.	2	6	14	7
Total abundance	1,718	2,109	1,698	1,088
Total number of species detected	49	49	49	46

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