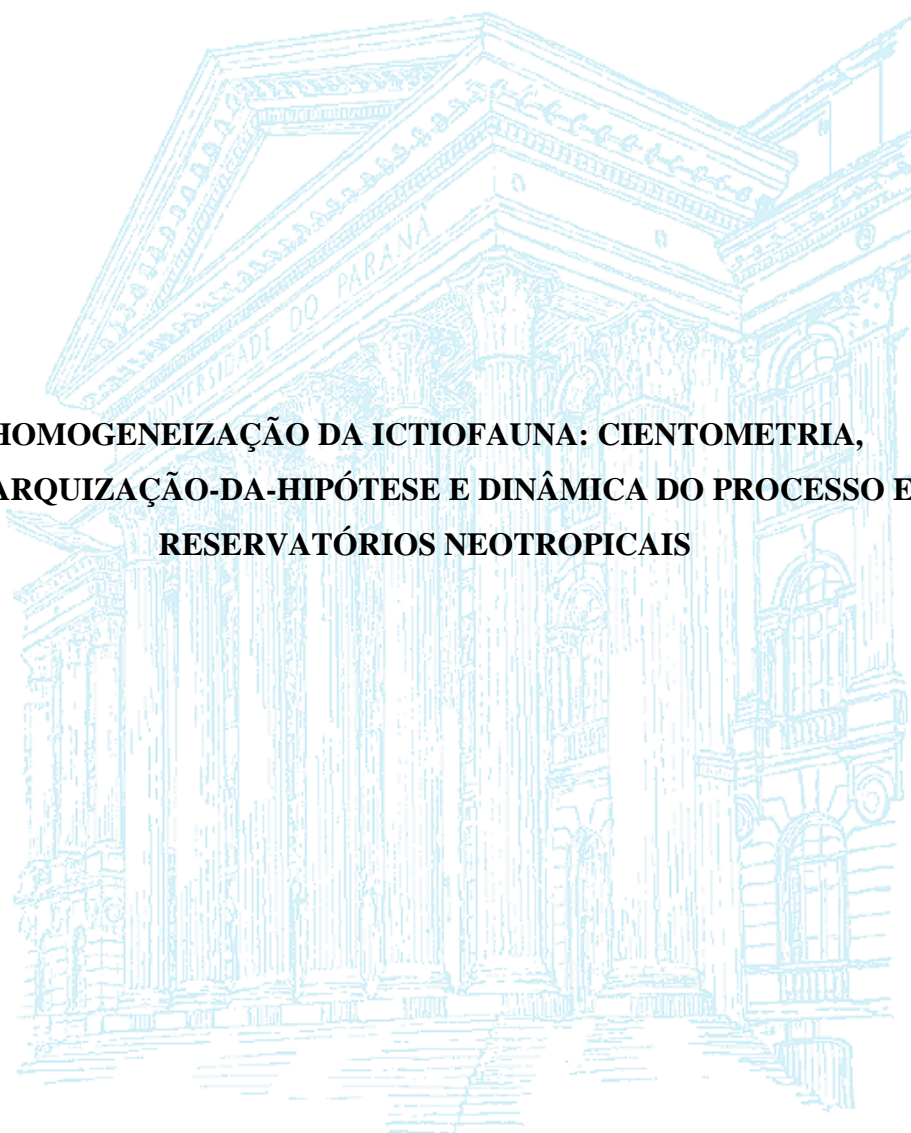**UNIVERSIDADE FEDERAL DO PARANÁ**

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS - ZOOLOGIA

VANESSA SALETE DAGA

HOMOGENEIZAÇÃO DA ICTIOFAUNA: CIENTOMETRIA, HIERARQUIZAÇÃO-DA-HIPÓTESE E DINÂMICA DO PROCESSO EM RESERVATÓRIOS NEOTROPICAIS

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Tese apresentada ao Programa de Pós-Graduação Ciências Biológicas – Zoologia, da Universidade Federal do Paraná, como requisito parcial para obtenção do título de Doutor em Ciências Biológicas, área de concentração Zoologia.

Orientador: Prof. Dr. Jean Ricardo Simões Vitule
Coorientador: Prof. Dr. Éder André Gubiani

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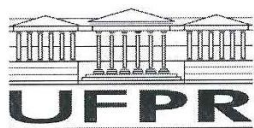
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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ZOOLOGIA da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **VANESSA SALETE DAGA** intitulada: **Homogeneização da ictiofauna: cientometria, hierarquização-da-hipótese e dinâmica do processo em reservatórios Neotropicais**, após terem inquirido a aluna e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO.

Curitiba, 15 de Março de 2017.

JEAN RICARDO SIMÕES VITULE
Presidente da Banca Examinadora (UFPR)

PITAGORAS AUGUSTO PIANA
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VICTOR PEREIRA ZWIENER
Avaliador Externo (UFPR)

Por unamidade esta banca recomendou a aprovação da professora Vanessa Salete Daga com distinção e louvor.

À minha família, especialmente
aos meus pais, por todo amor, carinho
e encorajamento. Minha eterna gratidão.

Ao Felipe Skóra (in memoriam),
por toda ajuda e incentivo. Gratidão.

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Ao Sr. Romeu e à Sra. Judi, por todas as palavras de carinho e incentivo nas horas difíceis.

"When we consider that the number of plants now found on the island [Saint Helena Island] is 746, and that out of these, fifty-two alone are native species, the rest being imported, and many of them from England, we see a good reason for this English character in the vegetation. The numerous species which have been so recently introduced can hardly have failed to have destroyed some of the native kinds. I believe there is no accurate account of the state of the vegetation at the period when the island was covered with trees; such would have formed a most curious comparison with its present sterile condition, and limited Flora. Many English plants appear to flourish here better than in their native country; some also from the opposite quarter of Australia succeed remarkably well. It is only on the highest and steepest ridges, where the native Flora is still predominant".

CHARLES DARWIN, July, 1836
(*Voyages of the adventure and Beagle*, 1839, p. 580)

"The entire destruction of its luxuriant native forests [Saint Helena Island] by the introduction of goats which killed all the young trees (a destruction which was nearly completed two centuries ago) must have led to the extermination of most of the indigenous birds and insects... Numerous imported birds, such as canaries, Java sparrows, some African finches, guinea-fowls, and partridges, are now wild. There are no native butterflies, but a few introduced species of almost world-wide range".

ALFRED RUSSEL WALLACE, 1876.
(*The geographical distribution of animals*, 1876, p. 269-270)

RESUMO GERAL

A homogeneização biótica é definida como o aumento da similaridade taxonômica, funcional ou genética, entre duas ou mais biotas ao longo do tempo. Este processo tem sido detectado em diferentes ecossistemas e diversos grupos de organismos, em especial para peixes de água doce. Entretanto, sua dinâmica permanece pouco esclarecida, principalmente quanto às escalas espaciais e temporais utilizadas e os mecanismos determinantes: introdução de espécies não-nativas, extinção de espécies nativas e modificações ambientais. Nesse sentido, dada à importância desse processo, faz-se necessária a síntese dos dados quantitativos de diferentes estudos, com o objetivo de encontrar generalizações, identificar as lacunas e direcionar estudos futuros. Sendo assim, foi utilizada a abordagem cienciométrica e o método de hierarquização-de-hipóteses, através do qual o processo de homogeneização biótica foi dividido em sub-hipóteses mais específicas. As regiões zoogeográficas Neártica e Paleártica apresentaram o maior número de artigos publicados relacionados ao processo de homogeneização biótica em peixes de água doce. Houve um maior número de artigos publicados avaliando o processo de homogeneização em rios, lagos e reservatórios, enfatizando que especial atenção deve ser destinada à riachos. A maioria das sub-hipóteses apresentaram observações suportando a homogeneização biótica. Quanto às formas de homogeneização, a maior parte das observações foi para a homogeneização taxonômica, sendo esta suportada em amplas escalas espaciais e temporais. Além disso, ficou evidente a escassez de estudos avaliando a dinâmica do processo em escalas temporais e espaciais mais refinadas. Adicionalmente, buscando avaliar a dinâmica do processo em reservatórios Neotropicais, a quantificação da homogeneização biótica em diferentes escalas temporais e espaciais mostrou que, na escala interbacias ocorreu homogeneização biótica devido, principalmente, à introdução e estabelecimento das mesmas espécies não-nativas na maioira dos reservatórios (i.e. espécies com alta pressão de propágulos como tilápias). Enquanto em escala intrabacias foi detectada diferenciação biótica, devido ao estabelecimento de diferentes espécies não-nativas em cada reservatório e a extirpação de espécies nativas. Por fim, devido a falta de estudos quantificando a dinâmica da homogeneização funcional na região Neotropical, a qual possui a maior diversidade funcional para peixes de água doce, buscou-se um melhor detalhamento e distinção dos principais aspectos desse processo em reservatórios. Para tal, a dinâmica das mudanças na composição de espécies e atributos funcionais foi avaliada, considerando diferentes

escalas temporais e espaciais. Na escala inter-ecoregiões, devido à introdução de espécies não-nativas com traços funcionais similares, e a perda de espécies nativas exibindo tanto traços similares como distintos, foi detectado o aumento da similaridade taxonômica (homogeneização taxonômica), enquanto ocorreu a diferenciação functional no primeiro período e, no último período a homogeneização funcional. Para a escala intra-ecoregião, para a maioria das ecoregiões avaliadas, foi detectada diferenciação taxonômica e functional, devido a introdução de diferentes espécies não-nativas, possuindo traços funcionais distintos. No entanto, nesta escala, para a ecoregião do Iguaçu, foi detectada diferenciação taxonômica enquanto houve homogeneização funcional, devido à extirpação de espécies nativas com traços funcionais distintos e, à introdução de diferentes espécies não-nativas funcionalmente redundantes.

Palavras-chave: diversidade beta; invasões biológicas; diferenciação biótica; ictiofauna; homogeneização funcional.

GENERAL ABSTRACT

Biotic homogenization is defined as the increase in the taxonomic, functional or genetic similarity, between two or more biotas over time. This process has been detected in different ecosystems and several taxonomic groups, especially for freshwater fish. However, its dynamics remain unclear, mainly regarding the spatial and temporal scales used and the determining mechanisms: introduction of non-native species, extinction of native species and environmental modifications. In this sense, given the importance of this process, it is necessary to synthesize quantitative data from different studies, with the aim of find generalizations, identify gaps and conduct future studies. Thus, was used the scientometric approach and the hypothesis-hierarchical method, through which the biotic homogenization process was divided into more specific sub-hypotheses. The zoogeographic regions Nearctic and Palearctic presented the largest number of published articles related to the process of biotic homogenization in freshwater fish. There was a greater number of published articles evaluating the homogenization process in rivers, lakes and reservoirs, emphasizing that special attention should be directed to streams. Most of the sub-hypotheses presented observations supporting the biotic homogenization. Related to the forms of homogenization, most of the observations were to the taxonomic homogenization, which was supported in wide spatial and temporal scales. In addition, it was evident the scarcity of studies evaluating the dynamics of the process in more refined temporal and spatial scales. Additionally, in order to evaluate the dynamics of the process in Neotropical reservoirs, the quantification of biotic homogenization at different temporal and spatial scales showed that biotic homogenization occurred at the interbasin scale, mainly due to the introduction and establishment of the same non-native species in most reservoirs (i.e. species with high propagule pressure such as tilapia). Whereas at intrabasin scale the biotic differentiation was detected due to the establishment of different non-native species in each reservoir and the extirpation of native species. Finally, due to the lack of studies quantifying the dynamics of the functional homogenization in the Neotropical region, which possess the greatest functional diversity for freshwater fish, it was sought a better detailing and distinction of the main aspects of this process in reservoirs. For this, the dynamics of the changes in the species composition and functional attributes was evaluated, considering different temporal and spatial scales. In the inter-ecoregions scale, due to the introduction of non-native species with similar functional traits, and the loss of native species

exhibiting each similar and distinct traits, the increase in the taxonomic similarity (taxonomic homogenization) was detected, whereas the functional differentiation occurred in the first period and, in the last period the functional homogenization. To the intra-ecoregion scale, for most ecoregions evaluated, the taxonomic and functional differentiation may be detected, due to introduction of different non-native species, with different functional traits. However, at this scale, to the Iguaçu ecoregion, taxonomic differentiation was detected while functional homogenization occurred, due to the extirpation of native species with distinct functional traits and, the introduction of different non-native species, which were functionally redundant.

LISTA DE FIGURAS

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Figure 1. Global distribution patterns of the articles related to biotic homogenization of freshwater fish communities and the percentage of the different types of biotic homogenization reported for each of the six zoogeographic regions. The broadened framework is represented by the letter B and the restricted framework is represented by the letter R. The graph in the top right represents the articles assessing biotic homogenization in all zoogeographic regions. Map modified from: Kreft and Jetz (2010). The coloured zoogeographic regions were represented as: Afrotropical (*brown*), Australian (*orange*), Nearctic (*green*), Neotropical (*purple*), Oriental (*yellow*) and Palearctic (*blue*).

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Figure 4. Temporal variation in the number of articles of the broadened framework (*white bars*) and restricted framework (*grey bars*) related to the biotic homogenization process, between 1995 and 2016 (a). Number of articles from the restricted framework (expressed as %) reporting the result of the homogenization dynamics, positive change (homogenization, *black bars*) or negative change (differentiation, *grey hatched bar*), in functional and taxonomic community similarity (b).

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Figure 8. Level of support based on weighted data for the sub-hypothesis spatial scale. Distinct letters on top of the bars indicate significant differences ($H_{3;85} = 18.39$; $P < 0.05$).

Figure 9. Schematic illustration of the HoH approach for the biotic homogenization process in freshwater fish faunas. The HoH was classified according to three criteria, as shown by hierarchical leves: 1) Type of biotic homogenization (Taxonomic or Functional); 2) Temporal scale (Finer: ≤ 10 years, and Large: > 10 years) and 3) Spatial scale (Small: < 1 km^2; Moderate (MOD): 1–100 km^2; Large: 101–1000 km^2; Very Large: > 1000 km^2). The boxes were color-coded (n ≥ 5) indicating the levels of support, using both weighted and unweighted data, as follows: *green boxes*: > 50.0% of weighted or unweighted data supporting the sub-hypothesis; *red boxes*: (if present it would indicate that), > 50.0% of weighted or unweighted data questioning the sub-hypothesis; *white*

boxes: all other cases (i.e. n < 5). *White boxes* with *green frames* represented sub-hypotheses with different results for weighted and unweighted data (here, weighted data were inconclusive and unweighted data supported the sub-hypotheses). *Green boxes* with *dashed frames* represented sub-hypotheses with different results for weighted and unweighted data (here, weighted data supported the sub-hypotheses while unweighted data were inconclusive). For exact values, see Tables S3 e S4 in Supplementary Material – Appendix 5.

Figure 10. Level of support based on weighted data for the mechanisms driving homogenization process. Distinct letters on top of the bars indicate significant differences ($t_{1;85)} = -0.89$; $P = 0.37$).

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Figure 12. Level of support based on weighted data for the zoogeopraphic regions. Distinct letters on top of the bars indicate significant differences ($F_{6;85} = 0.88$; $P = 0.50$).

Supplementary Material

Appendix 1

Figure S1. Flowchart representing the steps used in the systematic review and selection criteria for the articles searched in the ISI *Web of Science* (WoS) database. The questions represented the criteria for the selection of the articles in each stage of the screening.

Figure S2. Flowchart representing the steps of the elimination of non-relevant articles according to the first and second screening to this systematic review.

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Figure S5. Level of support based on unweighted data for the sub-hypothesis spatial scale. Distinct letters on top of the bars indicate significant differences ($H_{3;85} = 14.80$; $P < 0.05$).

Figure S6. Level of support based on unweighted data for the mechanisms driving homogenization. Distinct letters on top of the bars indicate significant differences ($t_{1;85} = -1.42$; $P = 0.15$).

Figure S8. Level of support based on unweighted data for the zoogeopraphic regions. Distinct letters on top of the bars indicate significant differences ($F_{6;85} = 1.66$; $P = 0.14$).

Chapter II

Figure 1 Location of the 20 reservoirs in three major basins in the State of Paraná, Southern Brazil. The different symbols represent the basins (*black stars* Coastal, *black circles* Iguaçu, and *black square* Upper Paraná). To more information about reservoirs see Table 1

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Figure 3 Variation in the percentage of non-native species in the State of Paraná from 2004 to 2007, at the interbasin and intrabasin scales. The different dashed lines represent the variation interbasin. The *dotted lines* represent the variation intrabasin. The *bold line* and *open squares* represent the mean (±SE)

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Figure 5 Beta diversity among basins/reservoirs overtime at the interbasin and intrabasin scales. Pearson correlations, P values, and linear correlations (if significant) between beta diversity and sampling period (*Su* summer, *Au* autumn, *Wi* winter, *Sp* spring) were showed on the graphics. N indicates number of sampling units used to estimate beta diversity

Chapter III

Figure 1 Location of the 20 reservoirs in three major freshwater ecoregions in the State of Paraná, Southern Brazil (ecoregions codes: 331, 344 and 346 according to Abell *et al.*, 2008). The different symbols represent the ecoregions (*black stars* Southeastern Mata Atlantica, *black circles* Iguaçu, and *black squares* Upper Paraná).

Figure 2 Mean changes in taxonomic similarity among reservoirs at inter-ecoregion and intra-ecoregion scales, for each time period. (a) Inter-ecoregion scale, (b) Southeastern Mata Atlantica, (c) Iguaçu, and (d) Upper Paraná ecoregions. Positive values represented taxonomic homogenization and negative values represented taxonomic differentiation.

Figure 3 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the inter-ecoregion scale ($n = 127$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similaritiesy in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

Figure 4 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the Southeastern Mata Atlantica ecoregion ($n = 6$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

Figure 5 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the Iguaçu ecoregion ($n = 36$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

Figure 6 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the Upper Paraná ecoregion ($n = 21$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which

taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

Figure 7 Mean changes in functional similarity among reservoirs at inter-ecoregion and intra-ecoregion scales, for each time period. (a) Inter-ecoregion scale, (b) Southeastern Mata Atlantica, (c) Iguaçu, and (d) Upper Paraná ecoregions. Positive values represented functional homogenization and negative values represented functional differentiation.

Figure 8 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the inter-ecoregion scale ($n = 127$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

Figure 9 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the Southeastern Mata Atlantica ecoregion ($n = 6$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

Figure 10 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the Iguaçu ecoregion ($n = 36$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

Figure 11 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the Upper Paraná ecoregion ($n = 21$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

Figure 12 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at inter-ecoregion scale for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

Figure 13 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at the Southeastern Mata Atlantica ecoregion for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

Figure 14 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at the Iguaçu ecoregion for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

Figure 15 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at the Upper Paraná ecoregion for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

Appendix 7 – Supplementary Material

Figure S1 Diagram of the steps of the statistical analyses for inter-ecoregion and intra-ecoregion scales. Taxonomic: 1a - The presence/ausence (P/A) data were converted into similarity matrices (using Jaccard's index), for each time period; 2a - Taxonomic similarity matrices (TS) were calculated for the initial assemblage ($TS_{initial}$) and for the assemblages sampled in each current period ($TS_{2002/2003}$, $TS_{2004/2005}$ and $TS_{2006/2007}$); 3a - Changes in pairwise taxonomic similarities were calculated between reservoirs at inter-ecoregion and intra-ecoregion scales for each time period, and measured as current similarity of a pair of reservoirs minus initial similarity of the same pair of reservoirs. Functional: 1b - The CWM reservoir-by-trait matrix was created, by multiplying the reservoir-by-species matrix and species-by-trait matrix for each time period; 2b - The CWM matrices were converted into similarity matrices (using Gower's distance); 3b - Functional similarity matrices (FS) were calculated for the initial assemblage ($FS_{initial}$) and for the assemblages sampled in each current period ($FS_{2002/2003}$, $FS_{2004/2005}$ and $FS_{2006/2007}$); 4a - Changes in pairwise functional similarities were calculated between reservoirs at inter-ecoregion and intra-ecoregion scales for each time period, and measured as current similarity of a pair of reservoirs minus initial similarity of the same pair of reservoirs. Adapted from: Pool & Olden, 2012.

Chapter II

Table 1 Characteristics of the reservoirs

Table 2 Frequency of occurrence of non-native species at the interbasin and intrabasin scales, and their vectors of introduction

Table 3 Model and number of parameters, values of Akaike information criterion adjusted (AIC_c), and difference between the model i and the best model (ΔAIC_c), for the best alternative models (i.e. $\Delta AIC_c < 2.0$) explaining beta diversity (β) trough different variables at the interbasin and intrabasin scales

Table 4 The importance value of each variable according to multi-model inference, and the standard coefficient of each variable in multi-model inference for all alternative variables explaining beta diversity at the interbasin and intrabasin scales

Appendix 6 – Supplementary Material

Table S1 Taxonomic identification of fish species sampled from the pristine sample (=P) and from entire period evaluated (2004 to 2007) for the ecoregions Coastal, Iguaçu and Upper Paraná basins. Status: N (native species for each respective basin), NN (non-native species from the same native biogeographic zone = extralimital in terms of ecoregion or basin) NN (non-native species from other biogeographical zones). The identification of species was based on Oyakawa et al. (2006), Graça & Pavanelli (2007), Baumgartner et al. (2012) and Bifi (2013). (Endemic species of Coastal basin = §; Endemic species of Iguaçu basin = * and Endemic species of Upper Paraná basin = Þ)

Chapter III

Table 1 Characteristics of the 20 reservoirs sampled

Table 2 List of life-history and ecological traits used to describe the fish functional composition

Appendix 7 – Supplementary Material

Table S1 Functional traits for 106 fish species

Table S2 Taxonomic identification of fish species sampled from the initial and current periods evaluated for the ecoregions Southeastern Mata Atlantica (SMA), Iguaçu and Upper Paraná. Status: *N* (native species for each respective ecoregion), *E* (native extirpated species = present in the initial dataset but absent at the dataset of the current periods), *NNT* (non-native species translocated from the same native zoogeographic region = extralimital in terms of ecoregion), *NNZ* (non-native species from other zoogeographic regions = extraregional introductions). The identification of species was based on Oyakawa *et al*. (2006), Graça & Pavanelli (2007), Baumgartner *et al*. (2012) and Bifi (2013). (Endemic species of Southeastern Mata Atlantica ecoregion = §; Endemic species of Iguaçu ecoregion = * and Endemic species of Upper Paraná ecoregion = Þ)

Table S3 Summary of taxonomic and functional similarities for historical and current periods. Temporal changes are indicated by the current value minus the initial one. Values are mean ± standard deviation and ranges in parentheses.

Appendix 8 – Scripts of the analyzes.

SUMÁRIO

INTRODUÇÃO GERAL

A distribuição geográfica das diferentes biotas foi, por muito tempo determinada por diversos fatores, como por exemplo, eventos geológicos, barreiras naturais e condições climáticas (Wallace, 1876; Vermeij, 1991), atuando em escala evolutiva. Dessa forma, eventos promovendo a mudança na distribuição de biotas não são recentes na história do planeta Terra, sendo o registro paleontológico repleto de exemplos, principalmente quando barreiras físicas foram removidas (Vermeij, 1991). Assim é o caso do soerguimento do Istmo do Panamá, há três milhões de anos, o qual permitiu a migração e mistura massiva de diferentes faunas, especialmente famílias de mamíferos, entre América do Norte e América do Sul, durante o Grande Intercâmbio Americano (Marshall, 1988; Vermeij, 1991; Roy & Kauffman, 2001). Atualmente, os padrões globais na distribuição da biota de diversos continentes têm sido ainda mais afetados pelas severas mudanças climáticas e, principalmente, devido ao efeito destrutivo exercido pela espécie humana no meio ambiente (e.g. Roy & Kauffman, 2001; McKinney, 2005; Ricciardi, 2007; Barnosky *et al*., 2011). As atividades humanas têm sido diretamente ligadas à extinção e introdução de espécies, causando o extermínio da megafauna através da caça, bem como a extinção de aves e mamíferos de pequeno porte, devido à predação por animais domésticos introduzidos em decorrência da colonização humana (e.g. Wilson *et al*., 2009; Vitule & Pozenato, 2012; Dirzo *et al*., 2014; Barlett *et al*., 2016).

A observação do impacto de espécies invasoras tem sido registrada desde o início do século XIX, por exemplo, Charles Darwin em sua viagem com o *Beagle*, em 1836, já notara na Ilha de Santa Helena, um grande número de espécies de plantas introduzidas, e que tais espécies dificilmente poderiam não ter destruído algumas espécies nativas (Darwin, 1839). Além disso, grande parte do atual conhecimento referente às participações humanas como agentes primordiais nos processos de modificação de biotas, foi devido às observações de Darwin em sua obra "*On the Origin of Species By Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*" (Ludsin & Wolfe, 2001). Posteriormente, inspirado pelas viagens de Darwin e outros naturalistas, Alfred Russel Wallace realizou diversas excursões, iniciadas aqui no Brasil por volta de 1848 e a partir das quais, propôs a divisão do mundo em seis regiões zoogeográficas (Wallace, 1876; Elton, 1958). Em seu livro "*The geographical distribution of animals*", Wallace relata para a mesma ilha visitada anteriormente por Darwin (Ilha de Santa Helena), a completa destruição das florestas nativas e a extinção

de aves e insetos, como uma consequência direta das introduções de espécies não-nativas pelo ser humano nas décadas precedentes (Wallace, 1876).

Pouco tempo depois, a introdução de diferentes espécies não-nativas tornou-se uma prática comum, especialmente devido a criação das Sociedades de Aclimatação, por volta de 1850, as quais tinham como principal objetivo a introdução, adaptação e domesticação de diversas espécies úteis e ornamentais, pelos continentes (Lever, 2011). Além disso, o comércio global transpôs as diferentes regiões zoogeográficas, aumentado as taxas de introdução e dispersão de espécies não-nativas à um ritmo demasiadamente acelerado, transformado a paisagem e, consequentemente, facilitando o processo de mistura entre biotas (Elton, 1958, Ricciardi, 2007). Diversos exemplos podem ser citados, como o Canal de Suez, construído em 1869 e ampliado em 2015 para a passagem de cerca de 100 navios por dia, permitindo, assim, a introdução e dispersão massiva de espécies não-nativas do mar Vermelho para o Mediterrâneo (Elton, 1958; Galil *et al*., 2014). O Canal do Panamá, inaugurado em 1914, liga o oceano Atlântico ao oceano Pacífico, sendo uma importante rota para o comércio marítimo internacional, permintindo a passagem de mais de 14 mil embarcações por ano, também servindo de corredor para a invasão de diversas espécies não-nativas (Wilson *et al*., 2009; Gollasch, 2011).

Dessa forma, graças às atividades humanas, um grande número de espécies foi transportado de uma região zoogeográfica para outra de maneira acidental, através da água de lastro (e.g. Padilha & Williams, 2004; Gollasch, 2011; Seebens *et al*., 2013), e/ou de forma intencional para fins de recreação/esporte, alimentação, controle biológico e ornamental (Lowe *et al*., 2000; Vitule *et al*., 2009; Brennan & Bryant, 2011). Diversos são os impactos decorrentes da introdução de espécies não-nativas, por exemplo, o *Myocastor coypus* (ratão-do-banhado), nativo da América do Sul, foi introduzido à nível global por volta de 1930, causando danos à agricultura, alterações dos ecossistemas aquáticos e levando à perda de habitat para diversos grupos, como plantas, insetos, peixes e aves (Carter & Leonard, 2000; Brennan & Bryant, 2011). Podemos citar ainda, o caso da cobra *Boiga irregularis*, nativa da Ilha de Papua Nova Guiné, a qual foi introduzida na Ilha de Guam, por volta de 1944, pouco depois da Segunda Guerra Mundial, provavelmente a bordo de cargueiros militares, causando a extinção da maioria das espécies de répteis e aves endêmicas da ilha, levando a efeitos negativos devastadores sobre a biodiversidade e o ecossistema como um todo, além de impactos econômicos e sociais (Savidge, 1987; Perry & Rodda, 2011; Stokstad, 2013). Outro exemplo catastrófico é o caso da perca-do-Nilo *Lates niloticus*, nativa das bacias hidrográficas de

Congo, Níger e Nilo, foi introduzida em 1954 no Lago Victória, África, a fim de incrementar a produtividade pesqueira; no entanto, levou à extinção de mais de 200 espécies de peixes endêmicas e à escassez das demais espécies, além de causar graves problemas ecológicos, econômicos e sociais (Lowe *et al.*, 2000; Vitule *et al.*, 2009; Cucherousset & Olden, 2011; Moyle & García-Berthou, 2011).

Dessa forma, a intensa eliminação de barreiras biogeográficas, juntamente com as demais ações antropogênicas como destruição de habitat, extinção de espécies nativas, bem como a translocação, introdução e dispersão de espécies não-nativas, têm levado ao empobrecimento biológico e à uniformidade da biota do planeta, resultando no processo denominado homogeneização biótica em escala global (e.g. Olden *et al.*, 2004; Olden, 2006; Ricciardi, 2007; Vitule & Pozenato, 2012; Liu *et al.*, 2017). A ideia de "homogeneização biótica" foi mencionada primeiramente por Charles S. Elton, em 1958, em seu livro "*The ecology of invasion by animals and plants*", como um processo complexo de aumento da similaridade entre biotas (Elton, 1958). Porém, o termo "homogeneização biótica" só foi precisamente definido cerca de quatro décadas após o livro de Elton, sendo descrito como a substituição da biota local por espécies não-nativas, normalmente introduzidas por humanos; causando assim, a substituição de espécies endêmicas raras por espécies amplamente dispersas (McKinney & Lockwood, 1999).

O primeiro estudo utilizando métricas simples de análise de similaridade foi realizado por Rahel (2000), no qual comparou a fauna histórica e atual de peixes nos Estados Unidos, encontrando que, em média, os pares de estados têm atualmente 15,4 mais espécies em comum, resultando em uma homogeneização média de 7,2%. Em 2001, ocorreu a publicação do livro intitulado "*Biotic Homogenization*", editado por McKinney & Lockwood, o qual possui 13 capítulos, discorrendo e avaliando o processo de homogeneização biótica para diversos grupos taxonômicos. Posteriormente, este processo foi proposto como o aumento da similaridade entre biotas ao longo do tempo (Rahel, 2002), sendo então definidas três formas de homogeneização biótica: taxonômica, funcional e genética (Olden *et al.*, 2004), e mais recentemente foi associado à perda de diversidade beta ao longo do tempo (Olden & Rooney, 2006). Além disso, este processo tem influenciado a uniformidade de todos os aspectos do mundo atual: biológicos, econômicos, culturais, sociais e tecnológicos (Lövei, 1997; McKinney & Lockwood, 1999; McKinney, 2005).

Dessa forma, como consequência das severas alterações ambientais, decorrentes de ações antropogênicas (e.g. McKinney, 2005, 2006; Olden *et al.*, 2006a; Smart *et al.*,

2006; Rahel, 2007; Solar *et al*., 2015), a introdução de espécies não-nativas cosmopolitas têm sido amplamente promovida (McKinney & Lockwood, 1999; Rahel, 2000; Olden & Poff, 2003; McKinney, 2004; Ricciardi, 2007), levando à extinção de espécies nativas (Rahel, 2000), e contribuindo assim para a atual crise da diversidade (McKinney, 2005). Adicionalmente, o processo de homogenização biótica tem sido detectado para os mais diversos grupos, como plantas (Smart *et al*., 2006; Winter *et al*., 2009), invertebrados (Holway & Suarez, 2006; Mori *et al*., 2015), peixes (Rahel, 2002; Petsch, 2016), anfíbios (Smith *et al*., 2009), répteis (Smith, 2006) e aves (Lockwood *et al*., 2000; Vallejos *et al*., 2016).

Dentre os diversos grupos em que o processo de homogeneização tem sido observado, peixes tem sido o mais amplamente utilizado para avaliar a dinâmica e detectar padrões do processo (Villéger *et al*., 2011; Hermoso *et al*., 2012; Toussaint *et al*., 2016a). Estudos acerca da similaridade entre ictiofaunas foram realizados utilizando diferentes escalas geográficas e períodos de tempo, nos Estados Unidos (Rahel, 2000; Olden & Poff, 2004; Marchetti *et al*., 2006) e no Canadá (Taylor, 2004), Europa (Clavero & García-Berthou, 2006; Hermoso *et al*., 2012), Ásia (Matsuzaki *et al*., 2013; Su *et al*., 2015), Austrália (Olden *et al*., 2008), Chile (Vargas *et al*., 2015) e Brasil (Petesse & Petrere Jr., 2012; Vitule *et al*., 2012; Daga *et al*., 2015). Entretanto, apesar do considerável número de estudos avaliando o aumento da similaridade entre as comunidades de peixes de água doce, as características desse processo permanecem pouco esclarecidas, principalmente quanto à dinâmica entre as escalas espaciais e temporais utilizadas e a importância dos mecanismos envolvidos no processo, como introdução de espécies não-nativas, extinção de espécies nativas e modificações ambientais (e.g. Olden, 2006). Adicionalmente, ecossistemas aquáticos de água doce podem ter perdido uma proporção ainda maior das suas espécies e habitats, quando comparados com ecossistemas terrestres e marinhos, especialmente devido às crescentes ameaças causadas por barramentos, irrigação, poluição e introdução de espécies (e.g. Casal, 2006; Dudgeon *et al*., 2006; Poff *et al*., 2007; Leprieur *et al*., 2008; Johnson *et al*., 2008; Clavero & Hermoso, 2011; Cucherousset & Olden, 2011; Vitule *et al*., 2015).

Atualmente, a homogeneização biótica tem sido considerada um dos principais desafios relacionados à conservação de peixes de água doce, destacando a importância de se quantificar os mecanismos condutores, biológicos e ambientais, bem como as consequências ecológicas deste processo (Olden *et al*., 2010). Dessa forma, com base no considerável número de artigos referentes ao tema e dada à complexidade desse

fenômeno, a presente tese se propõe a disponibilizar resultados que auxiliem na compreensão da dinâmica do processo de homogeneização biótica, integrando a revisão da literatura e síntese dos dados de diferentes estudos, visando elucidar o panorama geral sobre a homogeneização biótica da ictiofauna de água doce, gerando dados e informações úteis para estudos futuros. Além disso, dados empíricos referentes à comunidade de peixes em reservatórios Neotropicais foram avaliados, com o objetivo de quantificar a dinâmica das mudanças na composição de espécies e atributos funcionais em diferentes escalas espaciais e temporais, bem como identificar os principais mecanismos condutores desse processo.

No primeiro capítulo, com base em uma revisão sistematizada, foi utilizada a abordagem cienciométrica e o método de Hierarquização-de-Hipótese (HoH) (Heger & Jeschke, 2014), a fim de investigar o panorama atual sobre a homogeneização biótica de peixes de água doce. Dessa forma, pretendeu-se avaliar se a dinâmica das escalas espacial e temporal, bem como se a interação dos mecanismos determinantes no processo exerceram diferente influência sobre os diferentes tipos de homogeneização biótica. Além disso, buscou-se reconhecer as regiões zoogeograficas onde os estudos foram conduzidos, focando em identificar as regiões e/ou ambientes aquáticos nos quais deve ser atribuída maior atenção. Este capítulo é de coautoria de Raul Rennó Braga, Éder André Gubiani e Jean Ricardo Simões Vitule. O capítulo está nas normas e será posteriormente submetido à revista *Oikos*.

No segundo capítulo, pretendeu-se compreender a dinâmica do processo de homogeneização biótica em reservatórios Neotropicais. O objetivo foi identificar as espécies não-nativas e seus principais vetores de introdução, quantificar as mudanças espaciais e temporais na similaridade taxonômica das assembleias de peixes, bem como avaliar as mudanças temporais na diversidade beta de três bacias subtropicais. É de coautoria de Felipe Skóra (*in memoriam*), André Andrian Padial, Vinícius Abilhoa, Éder André Gubiani e Jean Ricardo Simões Vitule. Este capítulo foi publicado em março de 2015, em uma edição especial sobre espécies aquáticas invasoras na revista *Hydrobiologia*.

O terceiro capítulo, teve o objetivo de quantificar a dinâmica das mudanças na similaridade taxônomica e funcional de peixes em reservatórios Neotropicais. Para tal, foi considerado um conjunto de características funcionais, relacionadas à história de vida, uso de habitat, biologia e ecologia de peixes, as quais foram usadas para quantificar a extensão das mudanças na similaridade funcional de peixes em 20 reservatórios

distribuídos em três ecoregiões, utilizando diferentes escalas espaciais e temporais. Este capítulo é de coautoria de André Andrian Padial, Éder André Gubiani e Jean Ricardo Simões Vitule. O capítulo está nas normas e será posteriormente submetido à revista *Diversity and Distributions*.

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Biotic homogenization of freshwater fish: a global review

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ABSTRACT

Human activities have modified the Earth's biota, causing ecosystem disruptions due to habitat alteration and biological invasions, which, in turn, have led to the simplification of ecological communities, resulting in a phenomenon termed biotic homogenization. Biotic homogenization is defined as an increase in the similarity among a set of communities through time, reducing the diversity at any level of organization: taxonomic, functional or genetic. The purpose of this review is to summarize the existing information about the process of biotic homogenization in freshwater fish faunas to: understand its dynamics, patterns and implications, determine possible gaps in our knowledge, and draw broad generalizations. Scientometric and Hierarchy-of-Hypotheses (HoH) approaches were used to synthesize the information recovered through a systematic search of the literature. The literature search returned 1259 articles, of which 53 matched our selection criteria. The Nearctic region had the greatest number of articles published (20 articles), followed by the Palearctic and the Neotropical regions (17 and 6 articles, respectively). The journals *Diversity and Distributions*, *Global Ecology and Biogeography* and *Hydrobiologia* had the greatest number of publications on the topic. Thirty-one articles were analyzed using the HoH approach, which returned 85 observations of sub-hypotheses. Of these observations, 85% supported the biotic homogenization of freshwater fish, while 11% questioned it (i.e. detected differentiation). Most observations were related to taxonomic homogenization (88%), followed by functional homogenization (12%). With respect to the temporal scale, most observations were at the large scale, while to the spatial scale, most observations were at the large scale, followed by the small scale. This last result highlights the idea that biotic homogenization is dependent on different spatial and temporal scales. The larger scales led to the detection of functional and taxonomic homogenization. Finer scales led to the detection of both taxonomic homogenization and differentiation, due to greater probability of detecting introductions and extinctions of species. The main mechanisns driving the homogenization process in freshwater ecosystems were the introduction of non-native fish and habitat modification.

Keywords: scientometric approach, systematic review, biological invasions, biotic differentiation, ichthyofauna.

Introduction

Biotic homogenization has emerged recently as a fundamental concern for conservation biology (Olden et al. 2010). It often results in a decrease in the global biodiversity (Sax and Gaines 2003), thereby affecting community structure, as well as ecosystem functions and services (Foley et al. 2005, Dornelas et al. 2014, Mitchell et al. 2015, Magurran 2016). These changes are primarily a consequence of human-mediated habitat degradation and biological invasions (Lövei 1997, Sax and Gaines 2003, Stokstad 2005), which have severely altered the distribution of organisms worldwide (e.g. Ellis et al. 2013, Capinha et al. 2015, Bellard et al. 2016). Biotic homogenization has been defined as an increase in species similarity among communities through time, caused by the simplification of ecological communities through the replacement of regionally distinct native communities by range-expanding non-natives species (McKinney and Lockwood 1999, Rahel 2002, Olden and Poff 2003, 2004). On the other hand, some communities might become more different (i.e. decreased community similarity), leading to further biotic differentiation (Olden and Poff, 2003, 2004, Baiser and Lockwood 2011).

Currently, three distinct forms of homogenization may be taking place in any region. Taxonomic homogenization, which refers to the replacement of native species with non-native ones, increasing the species composition similarity among communities over time (McKinney and Lockwood 1999, Rahel 2002, Olden et al. 2004, Olden and Rooney 2006); functional homogenization, which refers to an increase in the functional similarity between two or more communities over time due to the establishment of a common suite of species with similar 'roles' in the ecosystem (e.g. non-native species that are functionally redundant), which replace species with unique functional 'roles' (i.e. specialists with no or little functional equivalent) (McKinney and Lockwood 1999, Olden and Rooney 2006); and genetic homogenization, defined as an increase in the genetic similarity between gene pools over time, which occurr through intraspecific and interspecific hybridization, thereby reducing the genetic variability within a species or among populations (Olden et al. 2004).

The process of biotic homogenization has been reported for the majority of the world's ecosystems (Baiser et al. 2012, Florencio et al. 2013, Dar and Reshi 2014, Magurran et al. 2015, Solar et al. 2015, Toussaint et al. 2016a). In addition, this process has been quantified for several taxonomic groups (Smith 2006, Cassey et al. 2007, Spear and Chown 2008, Horsák et al. 2013, Nascimbene et al. 2015, Solar et al. 2015). However,

many aspects of the biotic homogenization process remain incompletely known, specifically its dynamics at multiple spatial and temporal scales (Taylor 2004, Pool and Olden 2012), as well as those aspects related to the complex interactions of the distinct mechanisms of homogenization, the introduction of non-native species, the extinction of native species, and habitat alteration, although some predictions and generalizations have already been made (Rahel 2002, Olden and Poff 2003).

Most studies have focused on the homogenization process in freshwater fish, which is causing a global trend toward an increased taxonomic similarity across fish faunas (Rahel 2000, Clavero and García-Berthou 2006, Villéger et al. 2011, Petesse and Petrere Jr. 2012, Vitule et al. 2012, Su et al. 2015, Toussaint et al. 2016a). However, even for freshwater fish, the current state knowledge of this process is not well understood. Therefore, as part of our ogoing efforts to explore the dynamics and mechanisms leading to biotic homogenization/differentiation of freshwater fish communities, we conducted a review of the literature on the subject. The primary purposes of the review were to summarize the existing information, to achieve a greater understanding of the patterns and implications of this process, and to indicate major gaps and biases that should be the focus for future studies and further research efforts.

Freshwater fish communities were chosen to this review for several reasons. They were one of the first taxonomic groups to be evaluated for evidence of biotic homogenization. Therefore, there exist a considerable number of studies available focused on quantitative estimates of homogenization (Olden et al. 2016, Petsch 2016). Moreover, freshwater fish are among both the most diverse vertebrate groups and the most threatened faunas throughout the world (Duncan and Lockwood 2001, Reis et al. 2003; Dudgeon et al. 2006, Olden et al. 2010). The latter primarily the result of habitat destruction, overexploitation and the long history of the introduction of non-native fishes for a variety of human purposes (Dudgeon et al. 2006, Vitule et al. 2009, Cucherousset and Olden 2011). In addition, freshwater fishes will probably continue to be widely introduced and translocated at the same or considerably increased rates (Rahel 2002, Olden et al. 2010). The last fact is of great concern, since it may result in a further elimination of the biogeographic barriers and favor an even greater exchange of fish species among different freshwater regions, which, in turn would lead to the exacerbated loss of native species and an acceleration of the biotic homogenization process (Rahel 2007, Olden et al. 2010, Villéger et al. 2011).

In line with the purpose of this review, recent studies using a variety of methodologies and metrics have highlighted the importance of organizing scientific literature and information from multiple large-scale datasets in order to identify distinct areas, define sub-topics, and propose generalizations about a particular topic (e.g. Alba et al. 2014, Gallardo et al. 2016, Silva et al. 2016). Therefore, the scientometric approach, systematic reviews, and meta-analyses have all been commonly applied to large datasets in order to support research syntheses (e.g. Twardochleb et al. 2013, Lortie 2014, Cruz et al. 2016, Mercuri et al. 2016, Valduga et al. 2016). Recently, a new method for evaluating large datasets has been proposed. This method, termed the Hierarchy-of-Hypotheses approach, can be used to summarize and evaluate evidence for and against given ecological hypothesis (Jeschke et al. 2012, Heger and Jeschke 2014). In this approach, empirical studies of a broad hypothesis can be separated into hierarchically more specific sub-hypotheses, thus contributing to conceptual clarity and the development of new hypotheses and theories (Heger and Jeschke 2014).

In this context, in the present study we began with a systematic review of the literature with the goal of identifying relevant research articles related to the biotic homogenization process in freshwater fish communities. These were further analyzed with the main objectives of: *i*) verifying the geographical and temporal distribution of the studies; *ii*) evaluating which journals have the largest number of articles published on the subject; and *iii*) determining which freshwater habitats were the most studied. Then, based on this review, the Hierarchy-of-Hypotheses (hereafter HoH) approach was used to divide the biotic homogenization process on freshwater fish into different sub-hypotheses, with the aim of: *iv*) using the HoH approach to identify the dynamics and the main mechanisms of the biotic homogenization process, representing them as sub-hypotheses; *v*) relating the studies on the biotic homogenization process to the identified sub-hypotheses, *vi*) assessing the level of support of the different sub-hypotheses identified, and *vii*) detecting the possible gaps and drawing broad generalizations regarding the biotic homogenization process in freshwater fish communities, to recommend the direction to be taken in future studies.

Methods

Literature search and study selection

The literature search was conducted to identify articles published up to March 2016 using the Thomson Reuters database (ISI *Web of Science*, http://thomsonreuters.com/thomson-reuters-web-of-science/) and applying the following keywords combinations in the "Topic" search field: (*homogeni?ation* OR *differentiation* OR "*beta diversity*") AND (*freshwater*) AND (*fish*) (Fig. S1 in Supplementary Material - Appendix 1). The symbol "?" in the keyword "*homogeni?ation*" allows to find the terms written with variants of letters, in this specific case, words that may have been written with "*s*" or "*z*".

During the initial screening, titles and abstracts of the articles were analyzed in order to select publications related to the purpose of the present study. This screening resulted in the selection of potentially relevant articles, which were retained for further analysis. A second screening was conducted based on the full reading of the text of the articles selected previously. Studies that did not assess the biotic homogenization process in freshwater fish communities were excluded. The articles that met our selection criteria were classified as either:

      i) Broadened framework: articles that did not quantify homogenization *per se*, but did contain some sort of general evidence (comparatively weaker than more restrictive framework) of the biotic homogenization process on freshwater fish faunas (i.e. articles where the analyses were not based on species identities or did not examine the effects of time scales on community similarity) (*see* Olden 2006, Olden and Rooney 2006). These articles failed to account for how species composition changed over time, but it still provided insight into the overall level of homogenization.

      ii) Restricted framework: articles that assessed quantitatively the biotic homogenization process in freshwater fish faunas (i.e. articles that calculated the change in community similarity within a given time period and after an interval of time among two or more sites) (*see* Olden 2006, Olden and Rooney 2006). These articles provided estimates of the biotic homogenization process, since they assessed

species identity and quantified how species composition changed over time.

Therefore, for an article to be in our dataset, it had to assess qualitatively and/or quantitatively the biotic homogenization process or at least provide evidence of this process in freshwater fish faunas. In addition, the references cited in the articles returned by our search were also scanned, as well as articles cited in other reviews and meta-analyses. However, theoretical articles, meta-analyses and reviews were not included (Fig. S1 in Supplementary Material – Appendix 1).

Scientometric approach

For all articles that met our selection criteria, the following information was extracted: year of publication, journal, zoogeographical regions (proposed by Wallace, 1876: Afrotropical, Australian, Nearctic, Neotropical, Oriental and Palearctic), the main result of the homogenization dynamics, and type of freshwater habitat (classified into rivers, streams, lakes and reservoirs) where the study was performed.

The relative proportions of the different types of biotic homogenization were calculated according to zoogeographic regions and expressed as the relative frequency based on the number of articles reporting each biotic homogenization type versus the total number of articles. The relative frequency was calculated for articles classified as belonging to the broadened and restricted frameworks separately.

In order to determine which journals have published more articles related to the biotic homogenization, the distribution of articles (number of articles) by journal was calculated. However, the total number of articles published, by the different journals, in a given year varied considerably. Therefore, the more a journal publish the more likely it is to have published a paper on the given subject. Thus, aiming to verify which journals published more articles regarding biotic homogenization regardless of the total number of articles published for each journal, the relative weights (*w*) were calculated, using the equation suggested by Braga et al. (2012):

$$w = \left(\frac{n}{p \text{ x } e \text{ x } y}\right) \text{x } 1000$$

where: *n* is the number of papers selected from our survey for each journal, *p* is the average number of papers published in the first edition of each year, *e* is the average

number of editions per year, y is the number of years that the journal was published within our survey period (maximum value of 22 years because the first paper found was published in 1995 and the last in 2016).

In addition, to compare the patterns of temporal increase in the number of publications related to biotic homogenization of freshwater fish and non-native/invasive freshwater fish worldwide, a second search was conducted using the following keywords: (*inva* OR introduced OR alien OR exotic OR non-native OR non-indigenous*) AND (*freshwater*) AND (*fish*). The number of articles over time was calculated for biotic homogenization of freshwater fish communities and for non-native/invasive freshwater fish worldwide.

To assess the temporal trend of the articles related to the biotic homogenization process, the total number of articles on the topic, classified as belonging to the broadened and restricted frameworks separately, was counted for each year. Moreover, for the articles classified as belonging to the restricted framework, the number of articles reporting the result of the homogenization dynamics (i.e. homogenization or differentiation) was accounted and expressed as a percentage, showing the positive (homogenization) or negative (differentiation) change in community similarity. In addition, the total number of selected articles for each type of freshwater habitat was determined and classified as belonging to the broadened or restricted framework.

Hierarchy-of-Hypotheses

The HoH approach (Heger and Jeschke et al. 2014) was applied to the articles belonging only to the restricted framework. These were assigned to sub-hypotheses according to the following criteria:

1) *Type of biotic homogenization*

    At which level of organization were the changes in the biological distinctiveness among a set of communities through time evaluated:

    1.1) Taxonomic: evaluated using species presence/absence or abundance data to examine the degree of similarity in community composition;

    1.2) Functional: assessed based on the presence/absence of species traits or the frequency distribution of traits in the community;

       1.3)   Genetic: quantified as changes in genetic variability within a species or among populations of a species over time.

2) *Temporal scale*

The temporal extent of each article was divided into different time scales, classified according to time period commonly used to assess the dynamics of the homogenization process, as either:

      3.1) Finer ($\leq$ 10 years);

      3.2) Large (> 10 years).

3) *Spatial scale*

The spatial extent of each article ranged in grain size, classified according to Baiser et al. (2012) as either:

      2.1) Small (< 1 km^2);

      2.2) Moderate (1–100 km^2);

      2.3) Large (101–1000 km^2).

      2.4) Very large (> 1000 km^2).

Each combination of the above criteria was considered a sub-hypothesis of the broad biotic homogenization hypothesis. Most of the articles analyzed tested one or more sub-hypotheses. In addition, in order to have a full dataset retaining all possible information, every test of each sub-hypothesis was added separately. Therefore, the final number of the tests exceeded the number of selected articles in the restricted framework, since more than one test could be considered for a single article. For example, an article may have used different temporal scales to evaluate the biotic homogenization process in the same region. In this case, the article would result in different observations (i.e. different tests, one for each time series). The term *observations* was used hereafter for the HoH analyses. Following the HoH approach (Jeschke et al. 2012, Heger and Jeschke et al. 2014), each observation was classified as either supporting (observations were in accordance with the hypothesis, i.e. biotic homogenization), questioning (observations in conflict with the hypothesis, i.e. biotic differentiation), or undecided (observations were inconclusive). In the end, each observation provided information on all levels of sub-hypothesis.

For each observation resulting from articles of the restricted framework additional information was recorded: the mechanisms driving homogenization process (i.e. scenarios of invasion-only events or invasion-extinction events, according Olden and Poff 2003); geographic divisions (political or biogeographical divisions); spatial extent (classified as river basin, ecoregions, provinces, continent or global) and zoogeographical region (proposed by Wallace 1876) where the study was performed. For the spatial extent, a river basin was considered to be the smallest sample unit. When more than two river basins were analyzed we considered it to be an ecoregion, and when more than two ecoregions were analised we considered it to be a province.

Hence, each observation could differ according a variety of relevant aspects (e.g. type of scenario, spatial/temporal scales, spatial extent). These factors are extremely important when evaluating the biotic homogenization process. For example, when comparing the results of those observations resulting from articles of the restricted framework, more weight should be put on the results of observations that: 1) considered the invasion-extinction scenario, 2) evaluated their samples on a small spatial scale, 3) used, however, a large spatial extent (thus providing a large spatial scope of the study), 4) used a long time scale, and 5) considered biogeographic divisions.

Therefore, the observations resulting of the restricted framework were weighted according to these aspects, adapting the equation suggested by Heger and Jeschke (2014):

$$w = g \text{ x } h \text{ x } s \text{ x } e \text{ x } t$$

where: g is the score for geographic divisions (1 for political divisions and 2 for biogeographical divisions), h is the score for the type of scenario included (1 for species invasion-only scenario and 2 for species invasion-extinction scenario), s is the score for the spatial grain size of the dataset (1 for very large, 2 for large, 3 for moderate and 4 for small grain size), e is the score for the spatial extent of each dataset (1 for river basin, 2 for ecoregions, 3 for provinces, 4 for continent and 5 for global), and t is the score for the temporal scale evaluated (1 when changes in the community similarity were assessed over a period up to 10 years and 2 for changes assessed over a period of more than 10 years).

To assess whether the level of support differed between sub-hypotheses, statistical tests were performed with both weighted and unweighted data. For the weighted data, the proportional weight for each observation was calculated by dividing the weight of each observation separately (weights supporting, questioning or undecided)

for a given sub-hypothesis by the total sum of weights of that same sub-hypothesis. The result was multiplied by the total number of observations of that sub-hypothesis (Heger and Jeschke 2014).

In order to test whether the level of support differed between sub-hypotheses, the one-way ANOVA was applied. We tested the assumptions of normality and homoscedasticity using the Levene's test. When the interaction effect of the one-way ANOVA was not significant, Tukey test was applied to determine which level differed. If assumptions of ANOVA were not met, the data were transformed to ranks (Quinn and Keough 2002), and then we applied the parametric ANOVA model to ranked data (Conover and Iman 1981), checking the homoscedasticity in the ranked data. If the assumptions were still not met, we used the similar non-parametric test (Mann-Whitney U-tests and Kruskal-Wallis; Zar 1999). Additionally, Chi-square tests (χ^2) were used to assess whether results of observations supporting, questioning or being undecided were equally distributed within each sub-hypothesis. If the χ^2-test was statistically significant, post-hoc binomial comparisons between supporting and questioning observations were performed for that sub-hypothesis.

Results

Scientometric approach

The initial literature search resulted in 1,259 articles, from which 279 passed the initial screening. A total of 53 articles matched our final selection criteria. Of these, 22 articles were classified as broadened framework and the remaining articles (31), were classified as restricted framework (Fig. S2 in Supplementary Material − Appendix 1). Among the zoogeographic regions, the Nearctic region had the greatest number of articles published (20 articles). Of these, nine articles were related to the broadened framework and 11 to the restricted framework. When considering the Nearctic region alone, 67% of the articles included in the broadened framework were related to taxonomic homogenization, with each of the other types of homogenization (genetic, functional and functional/taxonomic) accounting for 11% each. In the restricted framework, 91% of the articles were about taxonomic homogenization and 9% assessed functional/taxonomic homogenization simultaneously. The Palearctic region had 17 articles published, 10

included into the broadened framework and seven articles in the restricted framework. Among the broadened framework articles most were related to taxonomic homogenization (60%), followed by genetic homogenization (20%), functional homogenization (10%) and articles that assessed simultaneously functional/taxonomic homogenization (10%). Among the restricted framework articles, 86% of the articles were related to taxonomic homogenization and 14% assessed simultaneously functional/taxonomic homogenization (Fig. 1).

Six articles were published for the Neotropical region, two related to the broadened framework and four articles to the restricted framework. For the broadened framework, one article was related to genetic homogenization and one assessed taxonomic homogenization. For the restricted framework, three articles (75%) were related to taxonomic homogenization and 25% assessed functional/taxonomic homogenization simultaneously. The Oriental region had only three articles published, all related to the restricted framework, of which two articles (67%) assessed simultaneously functional/taxonomic homogenization and one article (33%) assessed taxonomic homogenization. For the Australian region, just one article was recorded (not represented on the map, Fig. 1), which was related to the restricted framework, and assessed taxonomic homogenization. Six articles assessed biotic homogenization in all zoogeographic regions, one related to the broadened framework and five articles to the restricted framework, of which 80% were related to taxonomic homogenization and 20% assessed, simultaneously, functional/taxonomic homogenization (Fig. 1).

Figure 1. Global distribution patterns of the articles related to biotic homogenization of freshwater fish communities and the percentage of the different types of biotic homogenization reported for each of the six zoogeographic regions. The broadened framework is represented by the letter B and the restricted framework is represented by the letter R. The graph in the top right represents the articles assessing biotic homogenization in all zoogeographic regions. Map modified from: Kreft and Jetz (2010). The coloured zoogeographic regions were represented as: Afrotropical (*brown*), Australian (*orange*), Nearctic (*green*), Neotropical (*purple*), Oriental (*yellow*) and Palearctic (*blue*).

The articles identified through the search were published in 30 journals, 10 articles in *Diversity and Distributions*, five in *Global Ecology and Biogeography*, four in *Hydrobiologia* and three in *Biological Conservation*. The journals *Ecological Applications*, *Ecological Indicators*, *Freshwater Biology* and *Biodiversity and Conservation* each published two articles (Fig. 2). The others journals published only one article each. The journals *Diversity and Distributions* and *Global Ecology and Biogeography* had the highest weights (4.96 and 2.57, respectively) among publications on the biotic homogenization process in freshwater fish faunas (i.e. highest number of publications on the topic relative to the total number of publications). The remaining journals with more than one publication had $w < 1.0$ (Fig. 2).
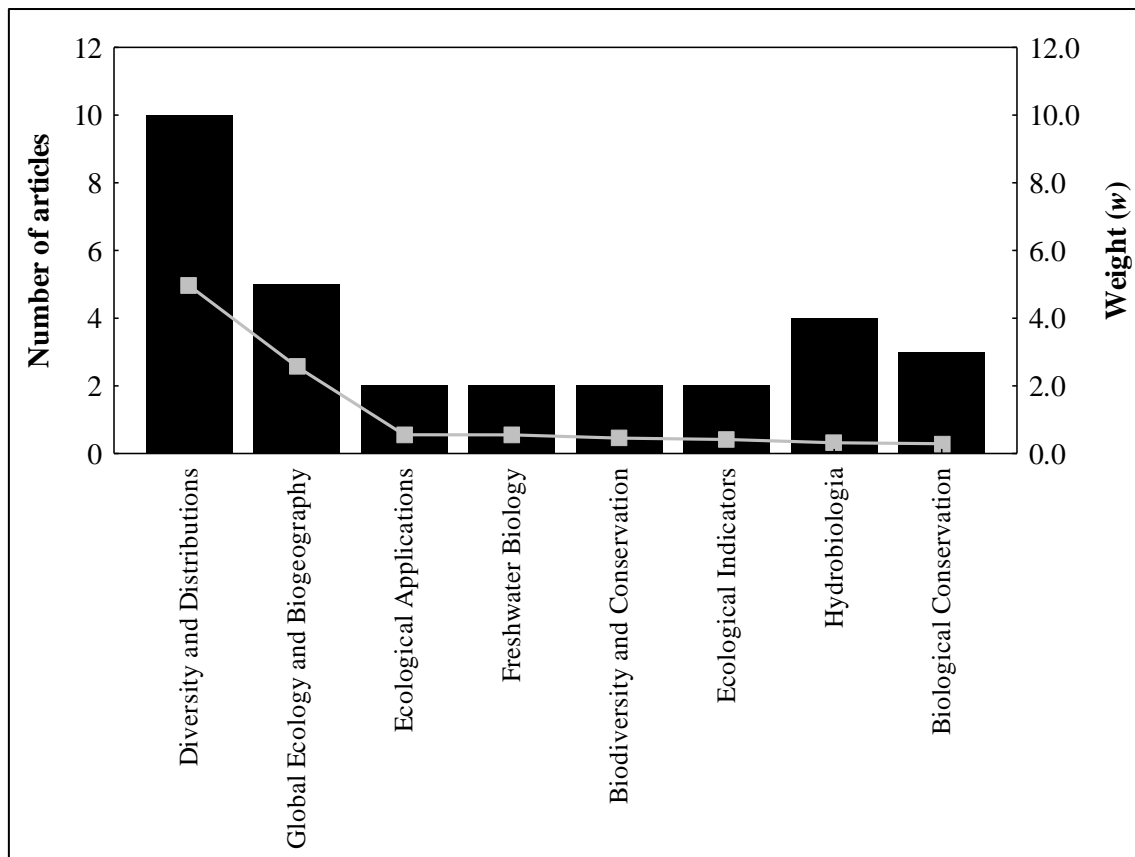
Figure 2. Distribution (number) of articles and the relative weights *w* (*grey line*) for each journal. The figure shows the journals with more than one publication.

The number of articles published related to homogenization process began to increase in the early 2000s, corresponding to the period immediately after the definition of the term biotic homogenization in 1999 (Fig. 3). The number of publications related to non-native/invasive freshwater fish worldwide varied more considerably after 2009. However, overall there was a pattern of increasing numbers of publications over time (Fig. 3). For the articles related to the process of biotic homogenization process in freshwater fish, the number of publications varied greatly over time. Even so, it also showed a definite pattern of increase over time (Fig. 3).
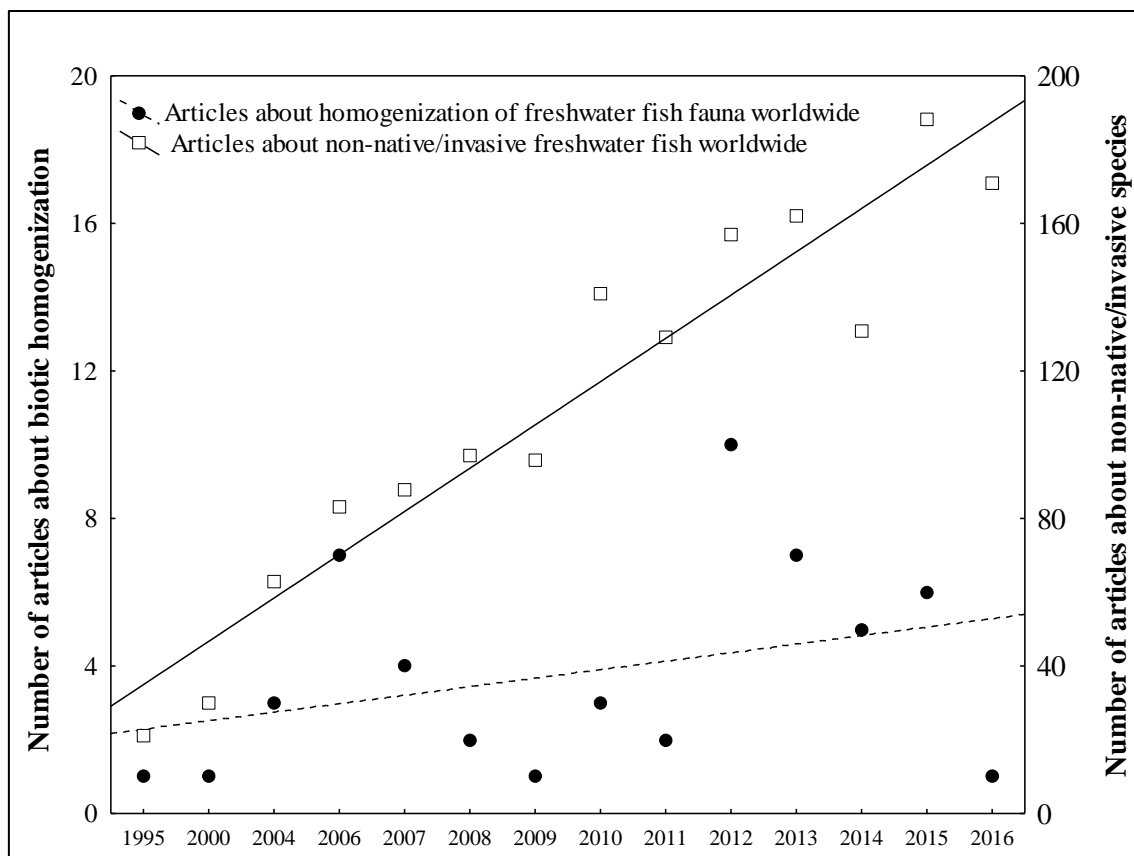
Figure 3. Temporal variation of the number of articles related to biotic homogenization in freshwater fish (*black circle*, *dashed line*) in comparison with the number of articles about non-native/invasive freshwater fish worldwide (*white square*, *solid line*), between 1995 and 2016. Please note the different scales of the two axes.

In the early 2000s, most of the articles were related to the broadened framework of the biotic homogenization process, while from 2008 most of the articles were about the restricted framework, which quantified changes in the pairwise community similarity between two time periods. In 2012 occurred the publication of the highest number of articles related to this framework, corresponding to seven articles (Fig. 4a). Most of articles related to the restricted framework documented an increase in taxonomic and functional homogenization of fish faunas through time, while a smaller number detected biotic differentiation (Fig. 4b).
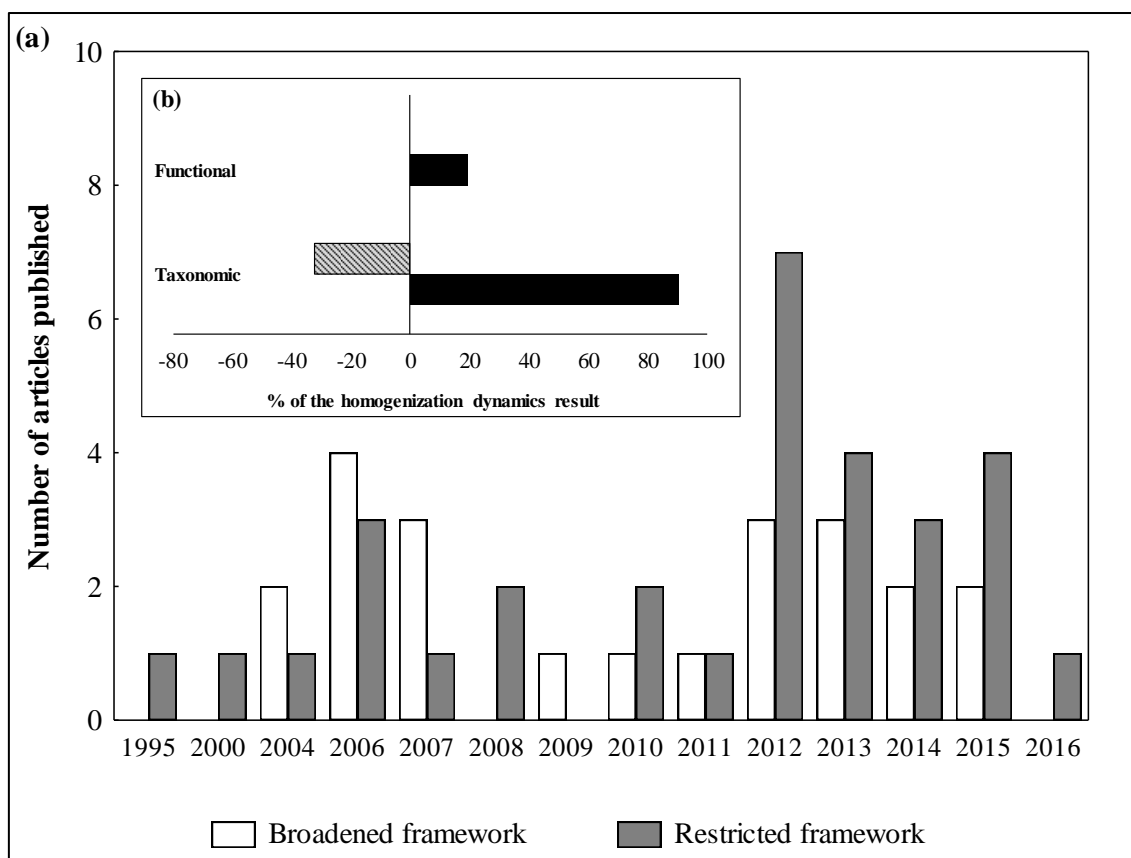
Figure 4. Temporal variation in the number of articles of the broadened framework (*white bars*) and restricted framework (*grey bars*) related to the biotic homogenization process, between 1995 and 2016 (a). Number of articles from the restricted framework (expressed as %) reporting the result of the homogenization dynamics, positive change (homogenization, *black bars*) or negative change (differentiation, *grey hatched bar*), in functional and taxonomic community similarity (b).

Most of the freshwater habitats were represented by a higher number of articles related to the restricted framework than to the broadened framework. Some articles did not distinguish between rivers, streams and lakes. These were considered as a single category, which had the greatest number of articles published (18 articles). Of these, seven articles were related to the broadened framework and 11 to the restricted framework (Fig. 5). However, the majority of the articles assessed specific types of freshwater habitats (rivers, streams, lakes and reservoirs) separately. Thirteen articles were published assessing biotic homogenization process in rivers. Of these, four articles were assigned to the broadened framework and nine articles were to the restricted framework (Fig. 5). Eight articles were published assessing biotic homogenization in streams. This category showed a inversed pattern in the number of publications, with five articles related to the broadened framework and three articles to the restricted framework (Fig. 5). Coincidentally, lakes and reservoirs each had seven articles published, with three

articles related to the broadened framework and four articles related to the restricted framework in each case (Fig. 5).
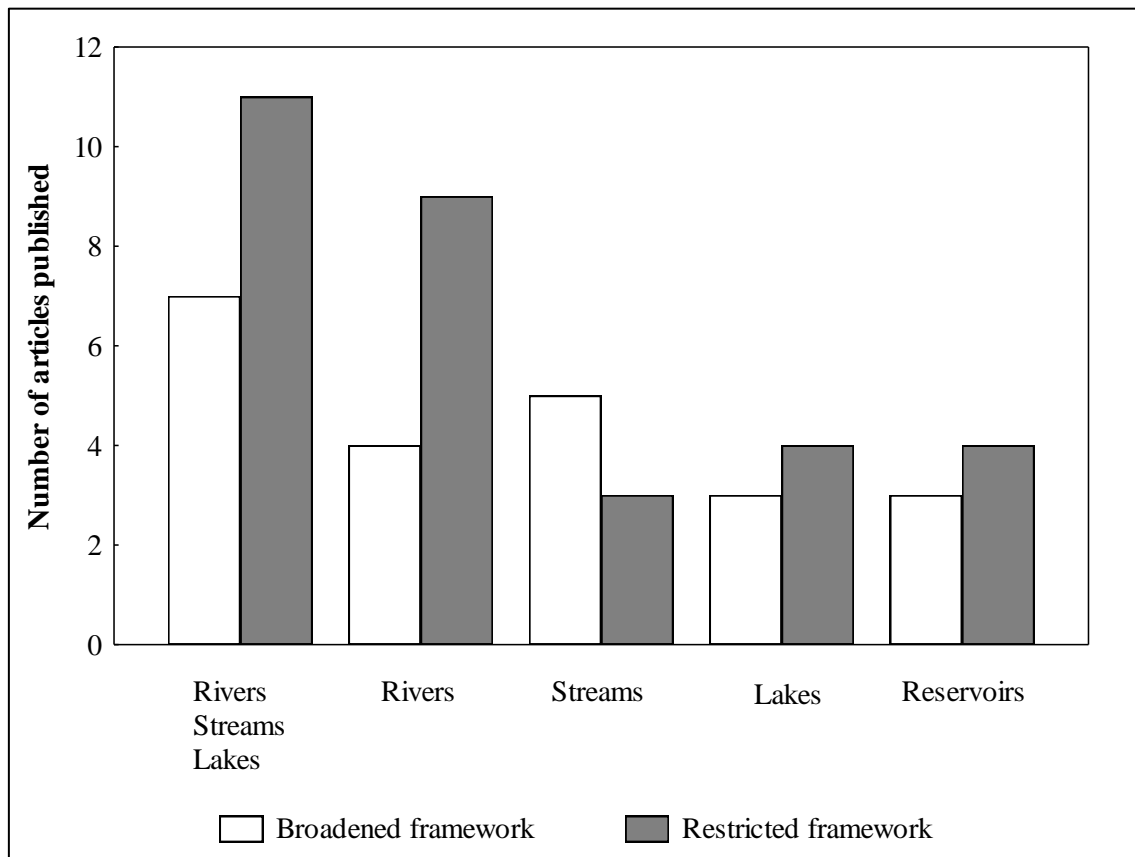
Figure 5. Number of articles of the broadened framework (*white bars*) and restricted framework (*grey bars*) according to each type of freshwater habitat.

HoH approach

The literature search identified 31 empirical articles, which included 85 observations of sub-hypotheses regarding to the biotic homogenization process in freshwater fish communities (Supplementary Material – Appendix 2). Of these observations, 85% supported biotic homogenization, while 11% questioned it (i.e. detect biotic differentiation) and 4% were undecided (Table 1). When unweighted observations were considered, a similar pattern was detected, with 76% supporting biotic homogenization, 19% questioning it and 5% were undecided (Table S1 in Supplementary Material – Appendix 3).

Regarding the type of homogenization, most of observations were related to taxonomic homogenization (88%, n = 75), followed by observations referring to

functional homogenization (12%, n = 10). Although no difference in the support level was detected between these two types of homogenization (Fig. 6), both presented a significantly larger number of observations supporting rather than questioning or undecided for weighted data (Table 1). Moreover, no studies quantifying genetic homogenization over time were identified by our search parameters.
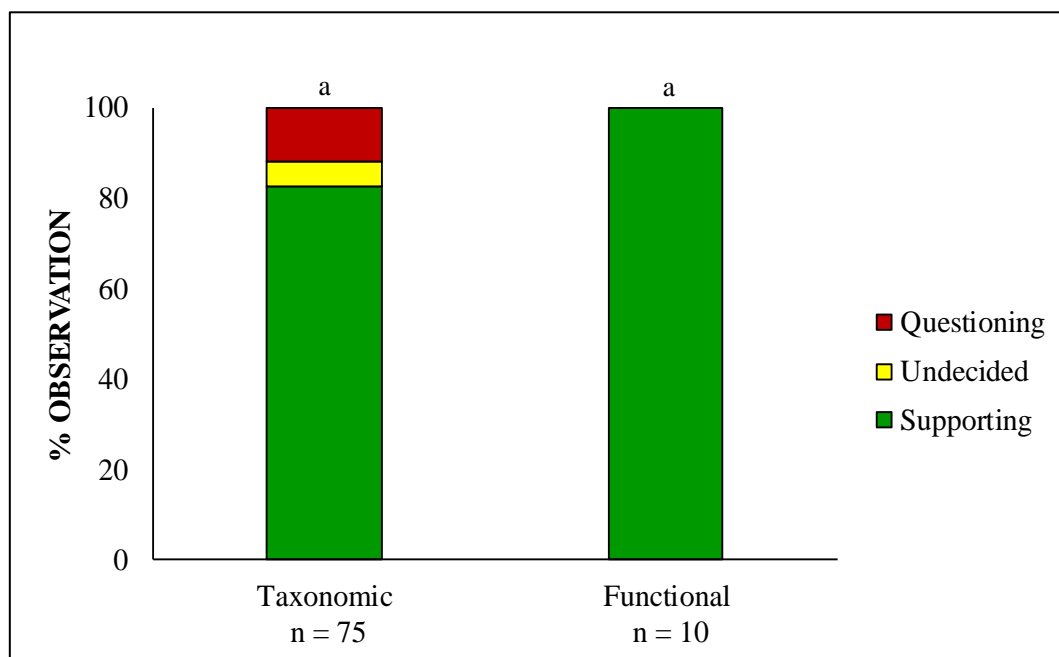
Figure 6. Level of support based on weighted data for the sub-hypothesis concerning the type of homogenization. Distinct letters on top of the bars indicate significant differences ($F_{1;85} = 1.77$; $P = 0.18$).

The majority of observations concerning temporal scales were related to the large temporal scale (89%, n = 76); only 11% (n = 9) of the observations deal with the finer temporal scale. Observations related to the large temporal scale showed a significantly higher level of support than finer temporal scale observations (Fig. 7). In addition, the large temporal scale had more observations supporting rather than questioning, whereas for the finer temporal scale there was no significant difference (Fig. 7, Table 1).

Table 1. Weighted data from observations supporting, questioning or undecided concerning the biotic homogenization process in freshwater fish communities, both for total and for each sub-hypothesis. χ^2 values indicate whether the distribution of the three categories differed from a uniform distribution. χ^2 was calculated only for comparisons with more than five observations. If significant ($P < 0.05$), post hoc binomial tests comparing the proportion of supporting versus questioning observations were performed. Significant results are in bold.

	n	Supported	Undecided	Questioned	χ^2	Binomial test
Total	85	85%	4%	11%	**<0.001**	**<0.001**
Taxonomic	75	83%	5%	12%	**<0.001**	**<0.001**
Functional	10	100%			-	-
Temporal scale						
Finer	9	45%	22%	33%	0.716	**-**
Large	76	88%	3%	9%	**<0.001**	**<0.001**
Spatial scale						
Small	24	50%	12%	38%	0.072	-
Moderate	9	78%	11%	11%	**0.018**	**0.043**
Large	34	97%		3%	**<0.001**	**<0.001**
Very Large	18	83%	6%	11%	**<0.001**	**0.002**

Figure 7. Level of support based on weighted data for the sub-hypothesis temporal scale. Distinct letters on top of the bars indicate significant differences ($U_{1;85)} = 188$; $P < 0.05$).

Regarding spatial scale, most observations still supported the biotic homogenization hypothesis. However, the majority of observations were for large and small spatial scales (40%, n = 34 and 28%, n = 24, respectively), followed by very large (21%, n = 18) and moderate (11%, n = 9) scales. Observations on large spatial scales showed much more support in comparison with the small spatial scale observations (Fig. 8). Overall, very large, large and moderate spatial scales had more observations supporting than questioning. However, for small spatial scales, observations showed no statistical differences in the number of observations supporting, questioning or undecided (Fig. 8, Table 1). When unweighted observations were considered, a similar pattern was detected; but at the small spatial scale the number of observations supporting and questioning were significantly higher than observations being undecided (Table S1 and Figure S5 in Supplementary Material – Appendices 3 and 4).

Figure 8. Level of support based on weighted data for the sub-hypothesis spatial scale. Distinct letters on top of the bars indicate significant differences ($H_{3;85}$ = 18.39; $P <$ 0.05).

In general, most sub-hypotheses related to the biotic homogenization process were widely supported, as illustrated by the HoH scheme (Fig. 9), while very few were questioned or undecided. With respect to the sub-hypotheses concerning the type of homogenization, we detected a distinct lack of observations at small temporal scales for the taxonomic and functional types of homogenization. Considering the taxonomic

homogenization type, most of observations on the lowest level of the hierarchy were supported. Nevertheless, the small spatial scale at the finer temporal scale was not supported when considering the weighted data (Fig. 9, Table S3 in Supplementary Material – Appendix 5). Similarly, the small spatial scale at the large temporal scale was not supported when considering unweighted data (Fig. 9, Table S4 in Supplementary Material – Appendix 5). These observations included those where the spatial and temporal dynamics of the biotic homogenization process were assessed, which led to the detection of taxonomic homogenization and differentiation; this scale presents a greater probability of detecting introductions and extinctions of species. Finally, for functional homogenization, most of observations were largely supported at large temporal and spatial scales (Fig. 9). In addition, this sub-hypothesis presented a lack of observations at smaller temporal and spatial scales.

Figure 9. Schematic illustration of the HoH approach for the biotic homogenization process in freshwater fish faunas. The HoH was classified according to three criteria, as shown by hierarchical leves: 1) Type of biotic homogenization (Taxonomic or Functional); 2) Temporal scale (Finer: ≤ 10 years, and Large: > 10 years) and 3) Spatial scale (Small: < 1 km^2; Moderate (MOD): 1–100 km^2; Large: 101–1000 km^2; Very Large: > 1000 km^2). The boxes were color-coded (n ≥ 5) indicating the levels of support, using both weighted and unweighted data, as follows: *green boxes*: $> 50.0\%$ of weighted or unweighted data supporting the sub-hypothesis; *red boxes* (if present it would indicate that): $> 50.0\%$ of weighted or unweighted data questioning the sub-hypothesis; *white boxes*: all other cases (i.e. n < 5). *White boxes* with *green frames* represented sub-hypotheses with different results for weighted and unweighted data (here, weighted data were inconclusive and unweighted data supported the sub-hypotheses). *Green boxes* with *dashed frames* represented sub-hypotheses with different results for weighted and unweighted data (here, weighted data supported the sub-hypotheses while unweighted data were inconclusive). For exact values, see Tables S3 e S4 in Supplementary Material – Appendix 5.

With respect to the mechanisms driving the homogenization process, most of observations were related to the invasion-extinction scenario (72%, n = 61), followed by observations related to the invasion-only scenario (28%, n = 24). The invasion-extinction scenario had more observations supporting homogenization than the invasion-only scenario. However, no difference in the support level was detected between these two scenarios (Fig. 10). Moreover, both presented a significantly larger number of observations supporting rather than questioning or undecided for weighted data (Table 2). When unweighted observations were considered a similar pattern was detected. However, for the invasion-only scenario the number of observations supporting and questioning showed no statistical difference (Table S2 and Fig. S6 in Supplementary Material – Appendices 3 and 4).
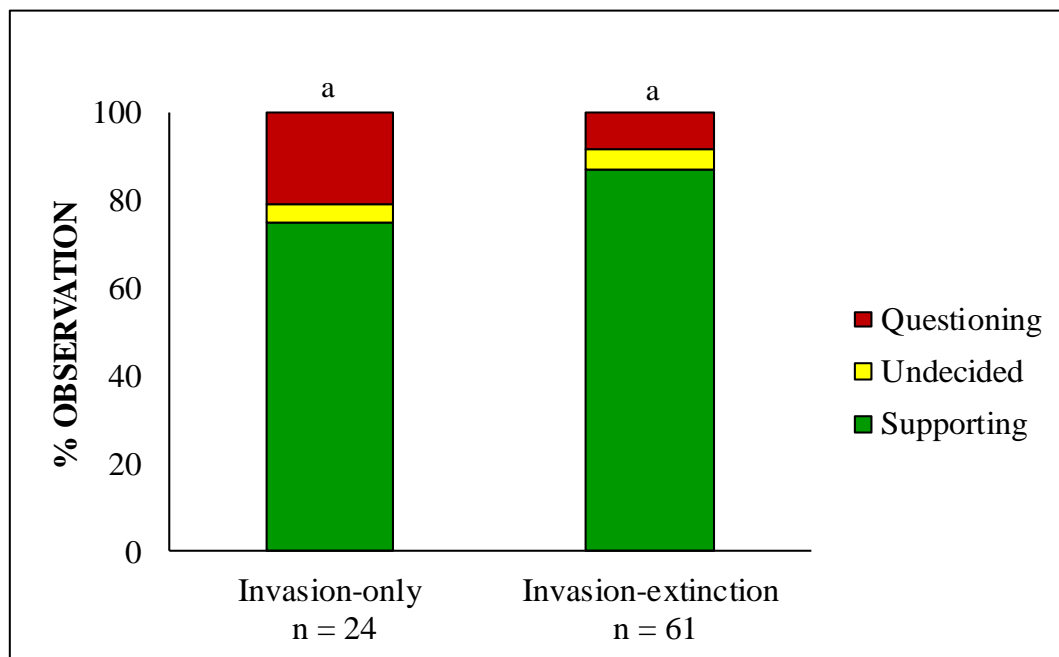
Figure 10. Level of support based on weighted data for the mechanisms driving homogenization process. Distinct letters on top of the bars indicate significant differences ($t_{1;85}$ = - 0.89; P = 0.37).

Regarding the spatial extent, continent (n = 27) and ecoregion (n = 21) had more observations, followed by province (n = 18), river basin (n = 16) and global (n = 3) spatial extents. The spatial extent differed in support level. Almost all of them were largely supported, the exception being the ecoregion spatial extent (Fig. 11). The global, continent, province and river basin spatial extent showed a significantly larger number of observations supporting rather than questioning biotic homogenization (Fig. 11, Table 2).

The ecoregion, in contrast, presented no statistical difference in the number of observations supporting, questioning or being undecided (Fig. 11, Table 2).
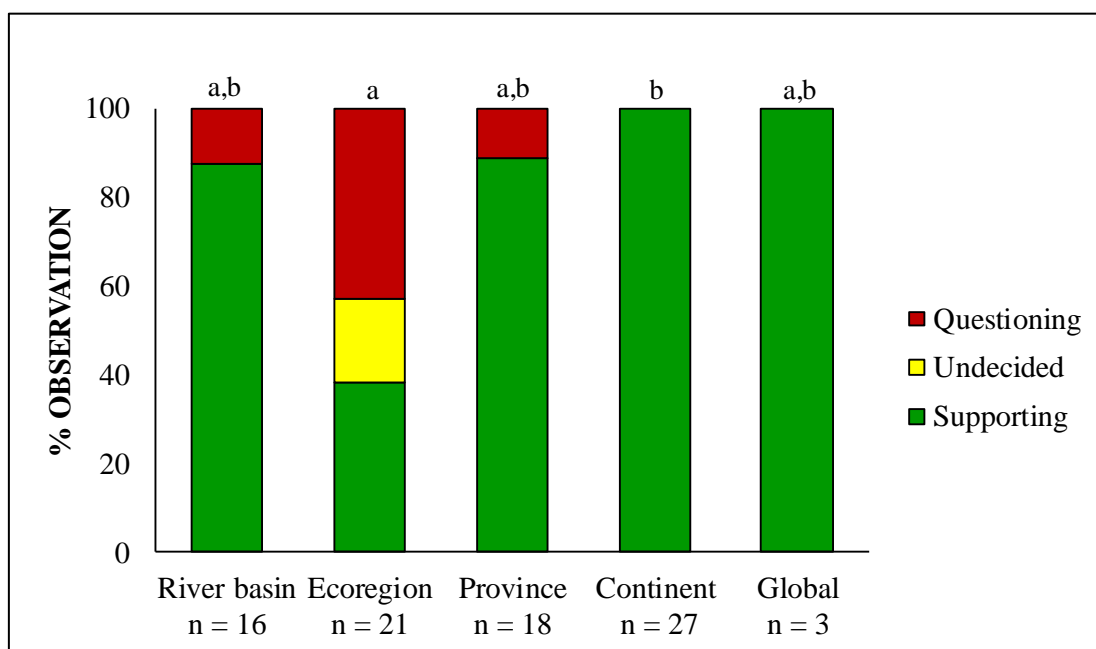
Figure 11. Level of support based on weighted data for the spatial extent. Distinct letters on top of the bars indicate significant differences ($H_{4;85} = 32.51$; $P < 0.05$).

Table 2. Weighted data from observations supporting, questioning or undecided about the biotic homogenization process in freshwater fish communities, differentiated according scenarios, spatial extent and zoogeographic region. χ^2 values indicated whether the distribution of the three categories differed from a uniform distribution. χ^2 was calculated only for comparisons with more than five observations. If significant ($P < 0.05$), post hoc binomial tests comparing the proportion of supporting versus questioning observations were performed. Significant results are in bold.

	n	Supported	Undecided	Questioned	χ^2	Binomial test
Scenarios						
Invasion-only	24	75%	4%	21%	**<0.001**	**0.007**
Invasion-extinction	61	87%	5%	8%	**<0.001**	**<0.001**
Spatial extent						
River basin	16	88%		12%	**<0.001**	**0.002**
Ecoregion	21	38%	19%	43%	0.367	-
Province	18	89%		11%	**<0.001**	**<0.001**
Continent	27	100%			**<0.001**	**<0.001**
Global	3	100%			-	**-**
Zoogeographic region						
Afrotropical	3	100%			-	-
Australian	5	80%		20%	0.075	-
Nearctic	31	81%	6%	13%	**<0.001**	**<0.001**
Neotropical	19	63%	5%	32%	**0.008**	0.162
Oriental	8	100%			-	-
Palearctic	16	88%	6%	6%	**<0.001**	**0.001**
all	3	100%			-	**-**

According zoogeopraphic regions, most of the observations were related to the Nearctic region (n = 31), followed by the Neotropical (n = 19) and the Palearctic (n = 16). Although no differences in the support level were detected among zoogeopraphic regions, most of them presented a significantly larger number of observations supporting rather than questioning or undecided (Fig. 12, Table 2). However, the Australian region presented no statistical difference in the number of observations supporting or questioning homogenization (Table 2), which may be due to the low number of studies in this region.
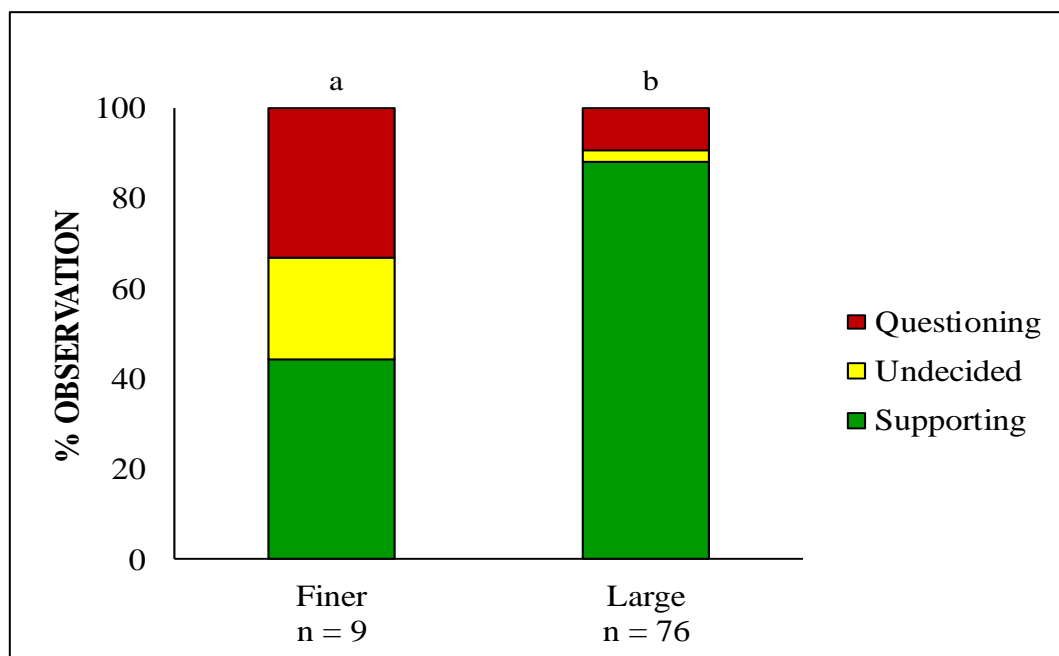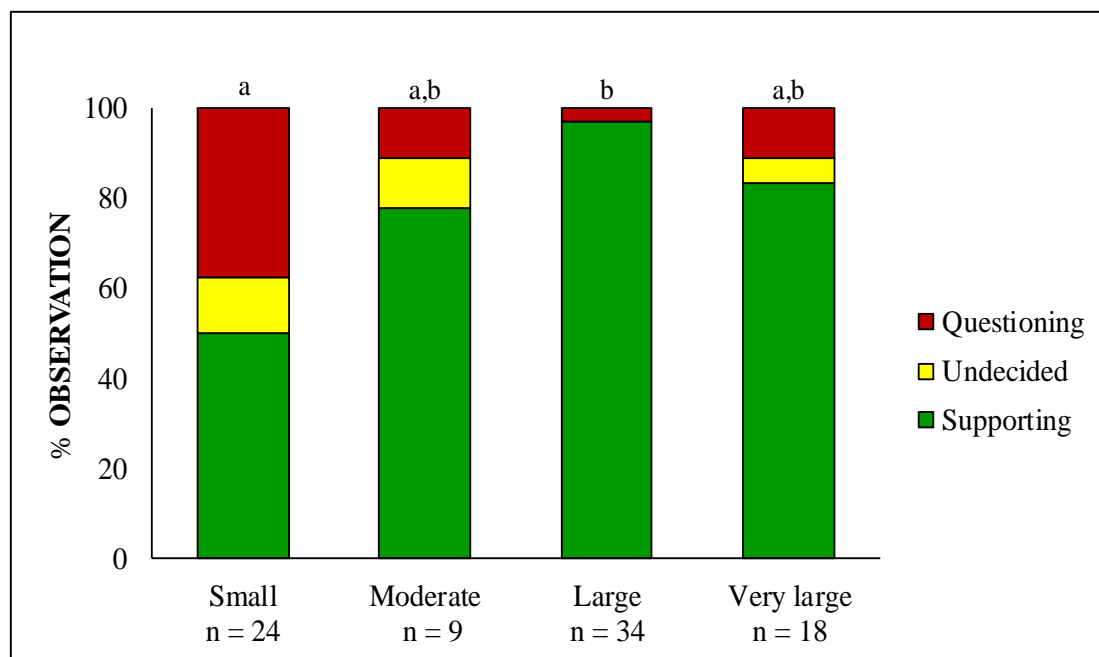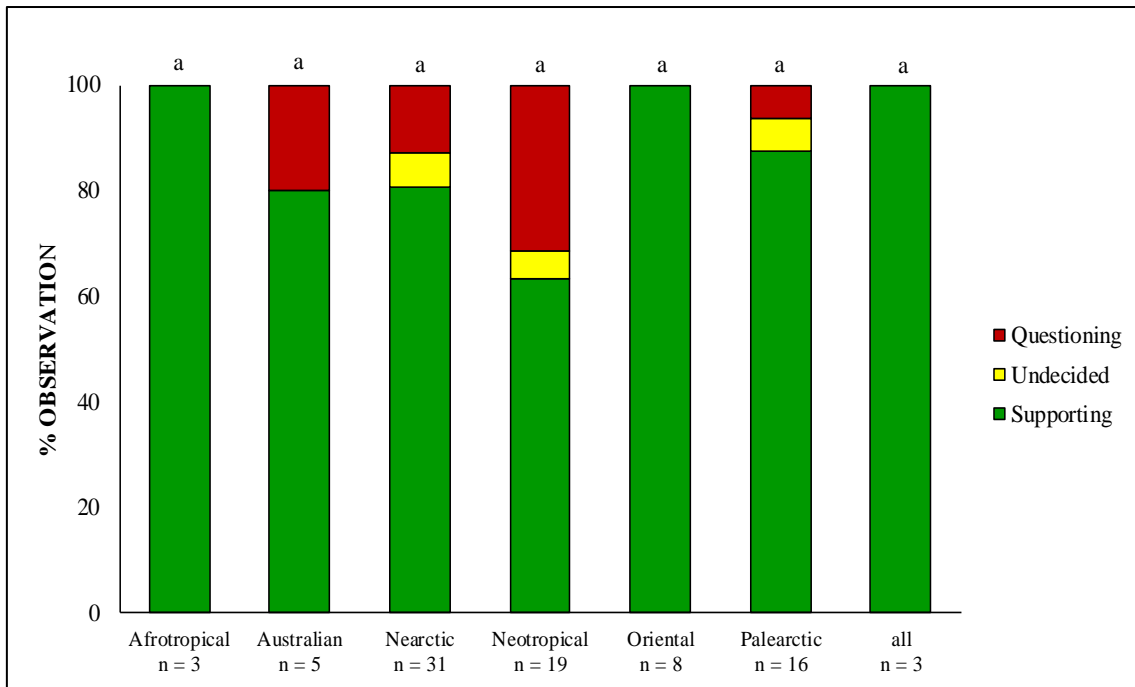
Figure 12. Level of support based on weighted data for the zoogeopraphic regions. Distinct letters on top of the bars indicate significant differences ($F_{6;85} = 0.88$; $P = 0.50$).

Discussion

In keeping with publications in other areas of research, our review showed that some zoogeographic regions were better represented than others. The Nearctic and Palearctic regions had the highest numbers of published articles related to the process of biotic homogenization in freshwater fish faunas; other regions have received less attention and, therefore, deserve additional research efforts. This bias does not seem to be restricted to the biotic homogenization process. The same bias can be seen, for example, in invasion biology (Lowry et al. 2013, Bellard and Jeschke 2016, Li et al. 2016). In addition, according to our review, taxonomic homogenization is the primary type of biotic homogenization studied across all zoogeographic regions, for both the broadened and the restricted frameworks, highlighting the need for more research on functional and genetic homogenization.

The majority of the articles used in our search were published in international journals, showing that biotic homogenization studies are of growing interest to the scientific community around the world. Our review also showed that although the number of articles about the biotic homogenization process in freshwater fish communities increased over time, it did not necessarily follow the same pattern of increase seen for articles written about non-native/invasive freshwater fish species. This fact may be the result of the short time period since biotic homogenization was first defined (McKinney and Lockwood 1999), toghether with the fact that the increase in the number of articles quantifying the homogenization process did not begin until about 10 years after the definition of the term. With the increasing attention given to this topic over the past few years and, with the increasing rate of introduction and dispersal of non-native fish species, we should expect more studies to be conducted concerning this topic as well as even higher global rates of biotic homogenization (Olden et al. 2010, 2016).

In general, a considerable number of articles were related to the broadened framework of biotic homogenization, which provides an overview of the biotic homogenization process. These articles only provide estimates of biotic homogenization, because they assessed species richness or examined the set of species at a single time point, without assessing community similarity at a previous time point (e.g. Olden et al. 2006a, Stainbrook et al. 2006). The greater number of articles in the restricted framework, increasing since 2008, quantifies an increase in taxonomic homogenization (e.g. Cheng et al. 2014, Su et al. 2015). However, some articles detected a decrease in the fish

community similarity over time, especially those describing the process at the finer scales. The finest dataset scales resolution increases the probability of detecting and/or observing the introduction and extinction of fish species, and thereby leads to detection of the biotic differentiation (Taylor 2004, Clavero and García-Berthou 2006).

Regarding the types of freshwater habitats most frequently assessed in studies of biotic homogenization, rivers, lakes, and reservoirs had the greatest number of articles published, usually related to the restricted framework. On the other hand, greater attention should be given to streams, which presented the lowest number of articles quantifying biotic homogenization (i.e. restricted framework). This freshwater habitat is often noted for its natural and pristine conditions, and for hosting several rare and endemic species. However, they are already severely affected by anthropogenic activities, ecosystem degradation, removal of riparian vegetation and introduction of non-native fish species with high invasive potential (Casatti et al. 2009, Magalhães and Jacobi 2013, Forneck et al. 2016, Teresa and Casatti 2017), which can all result in a further simplification of the fish fauna.

The HoH approach showed considerable differences in the number of observations assessing the sub-hypotheses of the biotic homogenizaton process in freshwater fish, as well as differences in the level of support for the sub-hypotheses. Overall, most of the sub-hypotheses had a greater number of observations supporting biotic homogenizaton, and it was independent of the unweighted or weighted data. However, despite the fact that most of the sub-hypotheses were well supported, some sub-hypotheses did have observations questioning the process (i.e. detecting biotic differentiation).

When we divided the biotic homogenization process into sub-hypotheses related to the type of biotic homogenization, most of observations assessing taxonomic and functional homogenization were supported, especially at large temporal and spatial scales. This pattern is in accordance with several studies, which have already detected taxonomic and functional homogenization of freshwater fish communities around the world (Marr et al. 2013, Cheng et al. 2014, Villegér et al. 2014). However, although taxonomic homogenization is usually better understood, it is possible that fish communities have become even more similar functionally (e.g. Buisson et al. 2013, Villéger et al. 2014). This is in line with our findings, in that most of the observations were focused on quantifying taxonomic homogenization, while studies quantifying the dynamic process leading to similarity in the functional characteristics of fish communities

have received less attention. In addition, at present there are not studies quantifying genetic homogenization over time, which may be linked to the recent development and use of molecular techniques.

The temporal dynamics of the biotic homogenization process can be divided into short and extended time scales. Overall, the increase in the taxonomic and functional community similarity was greater over larger time scales, in that the most of sub-hypotheses were largely supported. This fact can be associated with the establishment, spread and dominance of previously introduced non-native species, which can lead to biotic homogenization (Clavero and García-Berthou 2006, Petesse and Petrere Jr. 2012). On the other hand, we uncovered few observations related to biotic homogenization at finer temporal scales, all of them related to the taxonomic homogenization, and showing only a low level of support. Clearly the temporal dynamic of the biotic homogenization process deserves more attention, especially at finer scales. This is in accordance with the results of several studies, that indicate that working at finer scales led to the detection of biotic homogenization and differentiation, because of the increased probability of detecting changes in similarity through the continued introduction of several non-native species, which initially cause a reduction in community similarity, leading to biotic differentiation (Marchetti et al. 2001, Clavero and García-Berthou 2006, Petesse and Petrere Jr. 2012). Moreover, a few articles have, in fact, quantified the temporal dynamics of the biotic homogenization process. For example, one need only consider the observations in the articles from Clavero and García-Berthou (2006), Petesse and Petrere Jr. (2012) and Pool and Olden (2012), who found that the changes in the community similarity were dynamic over time. In these cases, the establishment of non-native fish initially resulted in biotic differentiation, while in the following years the expansion of populations of the previously introduced fish lead to biotic homogenization.

Regarding to the spatial scale, at large spatial scales, the changes in community similarity from the historical situation to the present-day were expected to be determined by the introduction of a common suite of non-native species, and by the discrete loss of native species, leading to biotic homogenization (Taylor 2004, Clavero and García-Berthou 2006, Petesse and Petrere Jr. 2012, Vitule et al. 2012, Toussaint et al. 2016a). At smaller spatial scales, the changes in community similarity between each pair of sites within a region become more apparent. This occurs because of the introduction of different non-native species and either no extinction or differential extinction of unshared native species, leading to the reduction in community similarity,

i.e. biotic differentiation (Marchetti et al. 2001, Olden and Poff 2004, Taylor 2004). This is in line with our findings, in that the most of observations supported taxonomic and functional homogenization at large spatial scales, while the observations at the small spatial scale showed a lower level of support, and only detected taxonomic homogenization.

The biotic homogenization process is driven by distinct mechanisms, which are the outcomes of several interactions between the extinction of native species, the introduction of non-native species and habitat modification (Rahel 2002, Olden and Poff 2003). Species invasions and extinctions can lead to different patterns of changes in community similarity (i.e. homogenization/differentiation), which can be even further accelerated by habitat modifications (Rahel 2002, Olden and Poff 2003, 2004). Our review showed that for the majority of the observations invasion-only and invasion-extinction events supported biotic homogenization of freshwater fish communities. These results were in agreement with the majority of studies quantifying the process of biotic homogenization, which have commonly evaluated the dynamics of the process considering invasion-only or invasion-extinction scenarios (Rahel 2000, Taylor 2010, Vitule et al. 2012).

Moreover, the biotic homogenization process can arise from species extinction-only, which although complex, uncommon and difficult to observe (Rahel 2000; Gillette et al. 2012), can occurs as a consequence of: *i*) species extinction due to environmental modifications, *ii*) species extinction due to the impact of the attempts of non-native species to establish themselves, even they are unsuccessful, and *iii*) species extinction due to predation/competition by other taxonomic groups (Rahel 2002, Olden and Poff 2003, 2004). Therefore, our findings confirm that the mechanisns resulting in the biotic homogenization process have yet to be fully understood, since there was more support for the invasion-only and invasion-extinction scenarios, while species extinction without species invasion has rarely been quantified (Rahel 2000; Gillette et al. 2012). Thus, future studies that assess this scenario should be encouraged, so that it can be better documented and understood through analyses at finer temporal and spatial scales.

The spatial extent might be another important factor for the biotic homogenization process in freshwater fish communities. Our results showed that within the broad spatial extent, biotic homogenization was largely supported, while the observations at the ecoregion extent showed lower level of support. This resulted from the pattern used by some articles in their site comparisons. In other words, some articles

used two levels of analysis, an initial broad subdivision for the comparison of sites between samples (as province or continent), and a second subdivision for the comparison of subsets of sites within a given sample (for example, ecoregions within the province). Moreover, the results on zoogeographic regions showed that for most of the regions the biotic homogenization had a high level of support, highlighting that this process is occurring on a global scale. However, there should be a greater concern and better understanding of the biotic homogenization process, especially in regions already under severe threat from invasion and human-mediated environmental degradation, which currently host high level of diversity, both taxonomic and functional (e.g. Marr et al. 2013, Toussaint et al. 2016b), and must be preserved in order to avoid further deterioration of their freshwater fish faunas and aquatic systems.

Conclusion

Previous reviews about biotic homogenizaton have already pointed out that different temporal and spatial scales, as well as the interactions among the introduction of non-native, the extinction of native species, and habitat modifications, can lead to differences in the dynamics of the biotic homogenization process. Our choice of the sub-hypothesis categories for our classification was driven by these previous reviews, and our results were largely in line with their conclusions about the biotic homogenization process. However, because these other reviews did not provide an organized quantitative compilation of the dataset, their goals were descriptive or theoretical. The main differences between our review and other reviews can be attributed to the fact that previous reviews included a low number of studies and/or had a restricted scope. Furthermore, the HoH approach demonstrated that when assessing the biotic homogenization process, it is useful to separete the main hypothesis into separate sub-hypotheses, which can be expanded and updated continuously. In addition, future studies on the biotic homogenization process require the inclusion of finer data resolution, in order to better assess and understand the dynamics of this process.

Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors

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"Unfortunately, Felipe Skóra, a very young PhD student, passed away while this paper was under review"

ABSTRACT

Non-native species introduced into reservoirs cause major changes in biodiversity, resulting in spatial and temporal biotic homogenization and/or differentiation. We used a sampling standardized temporally and spatially in reservoirs of basins located in the Neotropics, the Coastal, Iguaçu, and Upper Paraná basins. Our analyses were conducted at the interbasin and intrabasin scales, aimed at: (i) identifying the non-native species and their major vectors of introductions, (ii) assessing temporal and spatial changes in the fish assemblages, and (iii) evaluating temporal changes in the beta diversity of the basins/reservoirs. The spatial occupation of non-native species was variable, with *Tilapia rendalli*, *Cyprinus carpio* and *Oreochromis niloticus* the most frequently introduced species. This highlights aquaculture as the main vector of invasives on a large spatial scale. The percentage of non-native species at the interbasin and intrabasin scales increased over time. Temporal comparisons of the fishes support the hypothesis that biotic homogenization occurred at the interbasin scale, whereas the biotic differentiation was observed at the intrabasin scale. Beta diversity decreased over time at the interbasin and intrabasin scales, with decrease in species richness serving as the variable that best explained changes in biological diversity. There was no relation between beta diversity and time for the Iguaçu.

Keywords: Freshwater fish; Exotic species; Biological invasions; Extirpation of native species; Habitat alteration; Community ecology

Introduction

The multiple negative impacts associated with the introduction of non-native species have been the source of debate among ecologists for years (e.g. Gozlan, 2008; Vitule et al., 2009). The impacts are certainly context dependent (Vitule et al., 2012; Ricciardi et al., 2013; Simberloff & Vitule, 2014), so here is little doubt that additional research on the impacts of non-native fishes on biodiversity is a key element in the development of solutions to this complex global conservation issue (Cucherousset & Olden, 2011; Richardson & Ricciardi, 2013; Simberloff & Vitule, 2014; Dornelas et al., 2014). The accelerating changes in biota caused by multiple anthropogenic processes, such as extirpation, environmental modification, and the introduction of non-native species (Vitousek et al., 1996; Rahel, 2002; Devictor et al., 2008; Dirzo et al., 2014), can be seen in the homogenization and/or differentiation of various biological assemblages (Olden & Poff, 2003, 2004; Clavero & García-Berthou, 2006; Marchetti et al., 2006; Olden et al., 2008). Of the various anthropogenic processes at work, the introduction of non-native species and their subsequent invasions of adjacent areas are considered as major agents of global biotic homogenization (Clavero & García-Berthou, 2006; Rahel, 2007). This recently detected phenomenon is considered one of the least reversible of the global changes caused by humans (Kolar & Lodge, 2002; Ellender & Weyl, 2014).

Biotic homogenization and/or differentiation of freshwater fish fauna has been detected in systems from around the world (e.g. Rahel, 2000; Olden & Poff, 2004; Clavero & García-Berthou, 2006; Olden et al., 2008; Vitule et al., 2012). However, the effects of the introduction of non-natives into native biological assemblages are still unclear in poorly studied geographical regions. Although there is considerable literature showing that biotic homogenization is truly a multi-taxa global phenomenon (e.g. McKinney & Lockwood, 1999; Olden, 2006; Baiser et al., 2012), much remains to be learned about the spatial and temporal mechanisms' underlying patterns of homogenization. Therefore, it is important that various indicators quantifying homogenization and/or differentiation be used to measure and understand the process of change in ecosystems. Furthermore, the majority of the studies on biotic homogenization have been carried out in species-poor temperate regions (e.g. Villéger et al., 2011; Baiser et al., 2012). Currently, the magnitude of biodiversity in the Neotropical region is much greater, and, the rates of both habitat destruction and species loss are higher, than in

temperate regions (e.g. Magurran, 2011; Ellis et al., 2013; Dornelas et al., 2014), suggesting the potential for biotic homogenization may also be greater.

Human-induced environmental changes in freshwater ecosystems include the construction of dams, affecting the patterns of flooding, flow regime (Poff et al., 2007), sediment transport (Nilsson et al., 2005), trophic structure, and species composition (Allan & Flecker, 1993; Wellmeyera et al., 2005; Hoeinghaus et al., 2008; Ferrareze et al., 2014). Dams can also increase hydrologic connectivity between neighboring aquatic habitats, allowing the mixing of the fish fauna whose distributions were previously subject to geographic constraints from physical barriers (e.g. Tockner et al., 1999; Olden et al., 2010; Torrente-Vilara et al., 2011; Vitule et al., 2012; Clavero et al., 2013). The increased connectivity promotes the dispersal of fish into aquatic systems outside of their natural ranges, facilitating the human-mediated invasion of nonnative species (Havel et al., 2005; Agostinho et al., 2007; Johnson et al., 2008). Therefore, the major expected consequences due to dams construction are the increase in the establishment of introduced non-native fishes species (through translocations, stocking and hydrographic modifications) and the extirpation of endemic and endangered species or populations (e.g. McKinney & Lockwood, 1999; Rahel, 2000; Johnson et al., 2008; Petesse & Petrere Jr., 2012). In addition, the establishment of non-native fishes, and their subsequent invasion of new regions are more probable in disturbed systems where native assemblages have been disrupted (see Lockwood et al., 2007; Johnson et al., 2008).

The high diversity of the freshwater fish fauna in the Neotropics, the paucity of studies in the region, and the increasing human-mediated environmental degradation, highlight the importance of understanding the dynamics of biotic homogenization and/or differentiation processes and of knowing whether the principal drivers of these processes are truly non-native invaders or some other factor associated with Neotropical reservoirs. Our analyses were conducted at the interbasin and intrabasin scales, with the aim of: (i) identifying the non-native species and the major vectors of their introductions, (ii) assessing temporal and spatial changes in the fish assemblages, and (iii) evaluating temporal changes in the beta diversity of the basins/reservoirs. We expected that the presence of non-native fishes and the construction of dams would contribute directly to biotic homogenization at the interbasin scale and that the biotic differentiation might be observed at the intrabasin scale. Moreover, we expected that those basins/reservoirs with higher rates of species introductions would exhibit larger changes in beta diversity.

Materials and methods

Study area

The study area consisted of 20 reservoirs located in three major basins in the State of Paraná, Southern Brazil: the Coastal, Iguaçu, and Upper Paraná basins (Fig. 1; Table 1), each a part of a separate freshwater ecoregion according to Abell et al. (2008). The individual reservoirs studied have different flooding regimes, morphometry, water residence time, and uses, including public water supply, recreation, and energy production (Júlio Jr. et al., 2005; Gubiani et al., 2011).
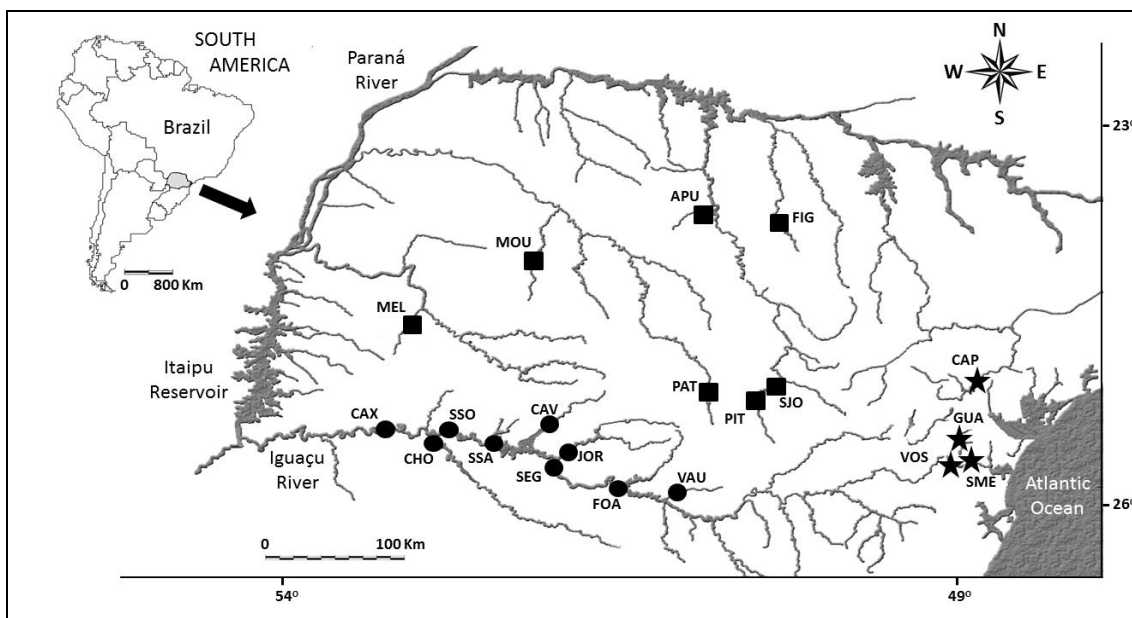
Fig. 1 Location of the 20 reservoirs in three major basins in the State of Paraná, Southern Brazil. The different symbols represent the basins (*black stars* Coastal, *black circles* Iguaçu, and *black square* Upper Paraná). To more information about reservoirs see Table 1

The Coastal basin, with a drainage area of 14,674 km^2 (Maack, 2012), includes coastal rivers originating in the highlands and in the eastern slope of the 'Serra do Mar' mountains and draining into the Atlantic Ocean. The Iguaçu River basin encompasses the largest drainage basin in the State of Paraná (approximately 72,000 km^2; Maack, 2012). The Iguaçu River can be divided into the upper Iguaçu, consisting of the segment extending from the source to the beginning of its rapids in Porto Amazonas (Ingenito et al., 2004); the middle Iguaçu, consisting of the stretch between Porto Amazonas and União da Vitória, where the third upland begins (Júlio Jr. et al., 1997); and

the lower Iguaçu, which is characterized by the presence of numerous waterfalls (Maack, 2012), this segment includes five large and several smaller reservoirs. The Paraná-La Plata basin (drainage area of 186,321 km^2; Maack, 2012), encompasses a complex of rivers draining into the interior of the continent. In the present study, we considered only the reservoirs from the Piquiri, Ivaí, and Tibagi rivers basins that belong to the upper reaches of the Paraná River basin. The Upper Paraná basin is composed of approximately the upper third of the Paraná River drainage, above the Itaipu reservoir. The Piquiri River rises in the 'Serra de São João', between the Ivaí and Jordão rivers; here, only one small reservoir was considered. The Ivaí River is formed by the junction of the São João and Patos rivers; in this study, two small reservoirs located on their tributaries were assessed. The Tibagi River has its source in the Campos Gerais region, and has few reservoirs, located primarily in its tributaries.

Sampling

We sampled fish assemblages quarterly from January 2004 to December 2007 in almost all of the reservoirs; in Salto Santiago and Salto Osório reservoirs, sampling was carried out monthly from January 2004 until July 2005, and bimonthly thereafter. However, the effort was standardized for all reservoirs by using only the information obtained in four coincident months per year (i.e. one month per season). We sampled using a set of gillnets with variable mesh sizes (2.4, 3, 4, 5, 6, 7, 8, 9, 10, 12, 14, and 16 cm between opposite knots) and trammel nets (mesh size: 6, 7, and 8 cm); the gillnets used were 10 to 20 m in width and 1.5 to 4.5 m in height. All gear was set for 24 h with inspections at 08:00, 16:00, and 22:00 Hrs. To avoid differences in the results caused by sampling, the data were standardized using catch per unit effort (CPUE).

After capture, the fish were killed using an overdose of the anesthetic benzocaine hydrochloride (250 mg/l), as recommended by AVMA (2001), then fixed in 4% formaldehyde, labeled and transported to the laboratory for analysis. Species identification followed Severi & Cordeiro (1994), Ingenito et al. (2004), Oyakawa et al. (2006), Graça & Pavanelli (2007), Menezes et al. (2007), and Baumgartner et al. (2012).

Table 1 Characteristics of the reservoirs

Reservoirs	Code	Geographic coordinates		Year of closure	Area (km^2)	Depth (m)	Transparency (m)
		Latitude	Longitude				
Capivari §	CAP	25°08'33.4"S	48°52'10.7"W	1970	12	43	2.4
Guaricana §	GUA	25°42'46.9"S	48°58'18.6"W	1957	7	17	1.9
Salto do Meio §	SME	25°48'32.8"S	48°59'39.6"W	1949	0.1	6.2	1.4
Vossoroca §	VOS	25°49'09.1"S	49°04'11.4"W	1949	5.1	12.5	2.6
Cavernoso *	CAV	25°29'31.6"S	52°12'50.2"W	1950	2.9	8.3	0.9
Chopim I *	CHO	25°34'23.6"S	53°06'51.9"W	1965	2.9	6	0.6
Derivação do Jordão *	JOR	25°45'15.0"S	52°04'52.9"W	1996	3.4	60	1.2
Foz do Areia *	FOA	26°00'22.2"S	51°39'15.5"W	1980	139	135	1.4
Salto Caxias *	CAX	25°31'41.1"S	53°29'14.7"W	1998	124	53	2.5
Salto Osório *	SSO	25°31'56.1"S	52°58'57.4"W	1975	55	40	2.7
Salto Santiago *	SSA	25°35'09.2"S	52°34'57.5"W	1979	208	70	2.0
Salto do Vau *	VAU	26°02'06.1"S	51°11'20.8"W	1959	2.0	3.5	1.8
Segredo *	SEG	25°47'36.1"S	52°07'13.9"W	1992	82.4	100	1.3
Apucaraninha Þ	APU	23°45'03.7"S	50°56'31.1"W	1958	2	13	0.6
Figueira Þ	FIG	23°51'07.6"S	50°23'19.9"W	1963	< 1	-	-
Melissa Þ	MEL	24°32'04.3"S	53°12'18.1"W	1962	2.9	5.3	0.2
Mourão Þ	MOU	24°06'34.9"S	52°20'05.9"W	1964	11.3	12.7	1.7
Pitangui Þ	PIT	25°01'39.6"S	50°06'09.7"W	1911	0.2	-	-
Rio dos Patos Þ	PAT	25°10'37.8"S	50°56'30.3"W	1949	1.3	5.8	0.4
São Jorge Þ	SJO	25°01'12"S	50°03'00.5"W	1945	7.2	-	-

§ Coastal; *Iguaçu; and ÞUpper Paraná basins, according to freshwater ecoregions of the world (Abell et al., 2008). The data were compiled from Júlio Jr. et al. (2005), Agostinho et al. (2007), Espíndola et al. (2010), and Gubiani et al. (2011)

Data analysis

We considered all taxa from each basin studied in our analysis (Table S1 in Supplementary Material). Native species were defined as those occurring in each region as a result of natural processes, while non-native species were extralimital species, species living outside their known natural range, that were introduced by a variety of mechanisms (e.g. aquaculture, sport fishing, and stocking). The data were analyzed at two different spatial scales. To assess changes at the interbasin scale, the 20 reservoirs of the three major sampled basins were considered. At the intrabasin scale, the reservoirs within each individual basin (i.e. the four reservoirs of Coastal basin; the nine reservoirs of Iguaçu basin; and the seven reservoirs of Upper Paraná basin) were considered.

Species diversity was expressed as species richness (number of species) for native, endemic, and non-native species at the interbasin and intrabasin scales. In addition, species richness of non-native species was also assessed according to the major

vectors of introductions, following Oyakawa et al. (2006), Graça & Pavanelli (2007), and Baumgartner et al. (2012). We calculated the percentage of non-native species captured during each year from 2004 to 2007, with the relative frequency based on the number of non-native species registered as a proportion of the total number of species at the interbasin and intrabasin scales.

We assessed the effects of non-native species on biotic homogenization and/or differentiation at regional scales (e.g. Harris et al., 2011) by assigning non-native species to categories of frequency of occurrence. The frequency of occurrence was based upon the number of reservoirs in which each species was collected (registered) as a proportion of the overall number of reservoirs at the interbasin and intrabasin scales.

Based on sampling data from 2002 to 2007 and on consultations with experts, we generated a species list indicating the most likely pristine assemblage for each aquatic system, consisting of native species only. The initial fish assemblages were estimated based on the data generated after the construction of the dam. Ideally, in order to evaluate the temporal changes caused by dams, the hypothetical pristine assemblage should consist of all species present before dam construction, since many species may have gone extinct after the alteration of their habitat (Olden & Poff, 2003). Locally extinct species were those that were present in the pristine list but absent from the 2004 to 2007 lists. Therefore, our scenario will be driven both by species introduction and by species extirpation (Olden & Poff, 2003).

Similarity matrices among the reservoirs were calculated at the interbasin and intrabasin scales, based on the presence/absence of fish species using Jaccard's coefficient (J):

$$J\left(x_1, x_2\right) = \left(\frac{a}{a+b+c}\right) \qquad (1)$$

where x_1 and x_2 are two sites with their fish assemblages, a is the number of fish species present in both sites, b is the number of species present only in x_1, and c is the number of species present only in x_2. This index ranges from zero (no similarity) to one (complete similarity) (Olden & Poff, 2003). Similarity matrices were calculated (Eq. 1) for the pristine assemblage, and for the assemblages sampled each year from 2004 to 2007, with the four samples collected each year pooled to form a single matrix. In the Salto do Meio reservoir, the fish assemblage was not sampled in 2005; comparisons between this reservoir and the others were not carried out for this year.

Changes in the similarity index for each pair of reservoirs can be used as indicators of homogenization or differentiation (Clavero & García-Berthou, 2006; Hermoso et al., 2012). If the result obtained by subtracting the similarity index for a pair of reservoirs from the similarity index calculated for the same pair of reservoirs during a later year is negative, then the assemblages have become less similar (more different), indicating biotic differentiation has occurred. On the other hand, if the result of the subtraction is positive, then reservoirs have become more similar, signifying biotic homogenization (Olden & Poff, 2003; Olden & Rooney, 2006; Olden et al., 2008).

We calculated changes in fish assemblage similarity indices at interbasin and intrabasin scales. First, at the interbasin scale, we quantified the biotic homogenization by evaluating changes in similarity index for each of the 127 pairwise comparisons considering only the reservoirs from different basins. Second, at the intrabasin scale, we calculated the changes in similarity index for each of the pairwise comparisons of the reservoirs within each individual basin; that is, six pairwise comparisons for Coastal basin, 36 pairwise comparisons for Iguaçu basin, and 21 pairwise comparisons for Upper Paraná basin. At finer spatial scales, the probability of detecting introductions and extirpation of species increases, resulting in the perception of biotic differentiation (e.g. Marchetti et al., 2001; Olden & Poff, 2003; Clavero & García-Berthou, 2006). In this sense, biotic homogenization may be more easily observed at the interbasin scale, while biotic differentiation may be more easily observed at the intrabasin scale (e.g. Marchetti et al., 2001; Olden & Poff, 2003; Clavero & García-Berthou, 2006). We calculated the change in Jaccard's Coefficient (Δ_J) between the initial pristine assemblage (P) and assemblages from each year from 2004 to 2007 (Δ_{JP}-2004, Δ_{JP}-2005, Δ_{JP}-2006, and Δ_{JP}-2007). As a general expectation, assemblages tend to become more similar even if the initial assemblage was already very similar (Olden & Poff, 2003, 2004). In this case, a positive linear relationship between initial assemblage similarity and Δ_J is expected. We also investigated temporal changes in the relationship between initial assemblage similarity and Δ_J, graphically. In this case, we had no theoretical expectations about how the relationship should change over time. On one hand, similar reservoirs may become even more similar over time, and dissimilar reservoirs may become even more dissimilar over time. If this is true we would expect that the positive linear relationship between initial similarity and Δ_J should increase from Δ_{JP}-2004 to Δ_{JP}-2007. On the other hand, similar reservoirs may become even more similar initially, but then begin to differentiate over time. In this case, positive linear relationship between initial similarity and Δ_J may

decrease from Δ_{JP}-2004 to Δ_{JP}-2007. Both scenarios have been suggested in previous studies (e.g. Olden & Poff, 2003; Clavero & García-Berthou, 2006).

Similarly, in terms of spatial distance, the geographically close reservoirs were expected to become more similar. This intuitive expectation of a decrease in species similarity with increasing distance is based largely on 'Tobler's law' (Tobler, 1970). Both initial similarity and geographical distance with Δ_J were plotted with the expectation of positive and significant linear relationships.

The biological heterogeneities of sampling periods were estimated by calculating beta diversity at each sampling period (summer, autumn, winter, and spring from 2004 to 2007). We calculated interbasin beta diversity at two spatial grain sizes. First, we calculated beta diversity at a large spatial grain size by estimating variation among basins, assuming one assemblage per basin (i.e. considering the overall variation of the ichthyofauna between basins). For this analysis, we pooled all species recorded for each basin in each sampling period and considered a basin-level grain size. Second, we calculated beta diversity at a smaller spatial grain size, considering each of the 20 reservoirs in the region separately (i.e. overall variation of reservoirs in Paraná State). In addition, we calculated intrabasin beta diversity for the reservoirs in each basin (i.e. overall variation of each basin): the four reservoirs of Coastal basin; the nine reservoirs of Iguaçu basin; and the seven reservoirs of Upper Paraná basin. Beta diversity, a measure of the variation in the assemblage structure, was estimated by the average distance of each basin/reservoir from the centroid in an ordination space based on the dissimilarity matrix (Anderson et al., 2011). Beta diversity is considered high in a certain sampling period, if the basins/reservoirs are more spread out in the ordination space. For these calculations, we used a Principal Coordinate Analysis (Gower, 1966) applied to the Jaccard dissimilarity matrix. Beta diversity, which reflects the overall dissimilarity of basins/reservoirs, was expected to decrease over sampling periods if biotic homogenization occurs.

The beta diversity of the basins/reservoirs over a period of time was assumed to depend on several factors. Periods with high species richness may also have high variation among basins/reservoirs. Similarly, if the average number of species per basin/reservoir is high, beta diversity should also be high. Introduced species may initially affect beta diversity in two ways: non-natives may promote homogenization (decrease beta diversity), if the same species are introduced in all basins/reservoirs; or they may promote differentiation (increase beta diversity), if different non-natives are introduced

into each basin/reservoir. Therefore, we used the total number of non-native species and the percentage of non-native species in the total assemblage as predictors of beta diversity. Furthermore, as the total number of exclusive native species in each basin/reservoir (those that occur in only one basin/reservoir, named here as 'uniqueness') increased, beta diversity was also presumed to increase. To evaluate which was the best predictor of beta diversity in basins/reservoirs, a process of model selection and multi-model inference were used to compare the likelihood of different models explaining beta diversity (Burnham & Anderson, 2002). Because we had no prior theoretical expectation of which combination of the variables should be used to generate alternative models to test, an exhaustive exploratory search of models was conducted, resulting in 31 possible models. However, we emphasize that the variables were chosen based on our understanding of the factors determining beta diversity.

Competing models included either one explanatory variable or a combination of explanatory variables. As a first step of the analysis, competing models were compared based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002). The model with the minimum AIC value was selected as the best. We then computed ΔAIC, the difference between the AIC of a given model and the AIC of the best model. Values of ΔAIC higher than 7 were considered indicative of models with poor fit relative to the best model, whereas values lower than 2 indicated models that are equivalent to the minimum (or best) AIC model (Burnham & Anderson, 2002). ΔAIC values were then used to compute the Akaike weight of each model (AIC_{wi}). Then, AIC_{wi} values were normalized across the set of candidate models to sum one, and they can be interpreted as the probability of a certain model to be the best. Coefficients of determination (R^2) were also calculated for each model as an indicator of the goodness-of-fit of the model. In a second step of the analysis, multi-model inferences based on model averaging were used to estimate the relative importance of each explanatory variable. These values are based on the AIC_{wi} of models in which a certain explanatory variable appeared (Johnson & Omland, 2004). For this reason, importance values should be interpreted as the contribution of an explanatory variable to the fit.

The vegan package (Oksanen et al., 2013) developed for the R language created for statistical computing and environmental analysis was used to generate dissimilarity matrices and to estimate beta diversity. Jaccard similarity matrices were used for Δ_J estimations by calculating 1 minus the dissimilarity matrix provided in ''vegdist'' function in ''vegan'' package. The SAM software, version 3.0 (Rangel et al., 2006) was

used for model selection and multimodel inference access. Values were considered significant when type I error was lower than 5%.

Results

Native species were distributed in five orders, 17 families, 44 genera, and 110 species; however, nine species only occurred in the pristine list. The number of native species varied from a low of 23 species in the Coastal basin to a high of 57 species in the Upper Paraná basin (Table S1 in Supplementary Material – Appendix 6; Fig. 2a). Forty-two species were considered endemic to their respective basins. Non-native species belonged to six orders, 12 families, 17 genera, and 24 species. Eleven of the non-native species were present in the Coastal basin, 21 in the Iguaçu and eight in the Upper Paraná basin (Fig. 2a). Nine non-native species were considered to have originated in other biogeographical zones (Table S1 in Supplementary Material – Appendix 6). The Iguaçu basin clearly had the highest number of both endemic and non-native species (Table S1 in Supplementary Material; Fig. 2a). On the other hand, the Upper Paraná basin had the highest richness of native species (Fig. 2a). The main vector of introduction was aquaculture, but non-natives were also introduced through baiting, sport fishing, and stocking activities (Fig. 2b). In the period from 2004 to 2007, the mean percentage of non-native species at the interbasin scale increased from 17.9% (range 7.7–26.5%) to 27.4% (range 12.3–37.5%) (Fig. 3). The total number of non-native species at the interbasin scale increased from 16 in 2004 to 24 in 2007. Similarly, the mean percentage of non-native species at the intrabasin scale increased from 19.8 to 26.3% for the Coastal basin, from 11.7 to 22.6% for Iguaçu, and from 8.2 to 12.3% for the Upper Paraná (Fig. 3).
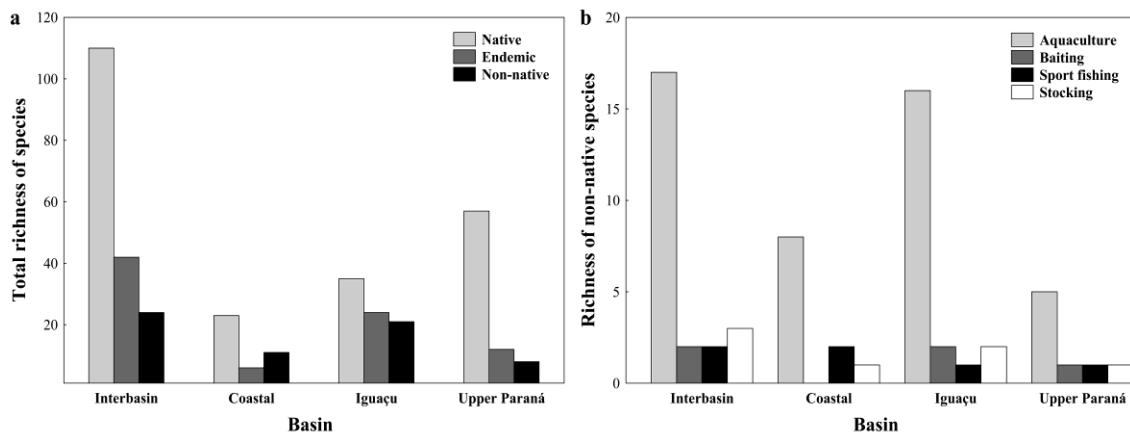
Fig. 2 Spatial variation of fish species richness at the interbasin and intrabasin scales. Total richness of species (a) and richness of non-native species according to the vectors of introductions (b)

The spatial frequency of occurrence (occupation) of the non-native species identified in this study was highly variable. However, at the interbasin scale, for over 50% of the reservoirs, the most frequently encountered species were *Tilapia rendalli*, *Cyprinus carpio*, and *Oreochromis niloticus*. On the other hand, at the intrabasin scale, for the Coastal basin, the most common non-native species were *Astyanax altiparanae*, *Micropterus salmoides*, and *T. rendalli*, which were present in all reservoirs in this basin. For the Iguaçu, *A. altiparanae* was present in all the reservoirs, while the species *Gymnotus inaequilabiatus* and *T. rendalli* were both found in 78% of the basin's reservoirs. Finally, in the Upper Paraná basin, *G. sylvius*, *O. niloticus*, *C. carpio*, and *T. rendalli* occurred in more than 50% of the basin's reservoirs (Table 2).

Changes in the similarity of the fish assemblages over time depended on the spatial scale examined. When changes in similarity were evaluated at the interbasin scale, the metric Δ_J was positive for most of the pairwise comparisons; that is, there was the increase in similarity among fish assemblages, indicating biotic homogenization (Fig. 4). Generally, there was a positive association between initial similarity of the assemblage and Δ_J, showing that reservoirs initially little similar became more similar over time. However, this association was significant only when the comparison was made between the pristine assemblage and assemblages sampled in 2006 and 2007. The homogenization and/or differentiation patterns could not be explained by the geographic proximity of reservoirs (Fig. 4).
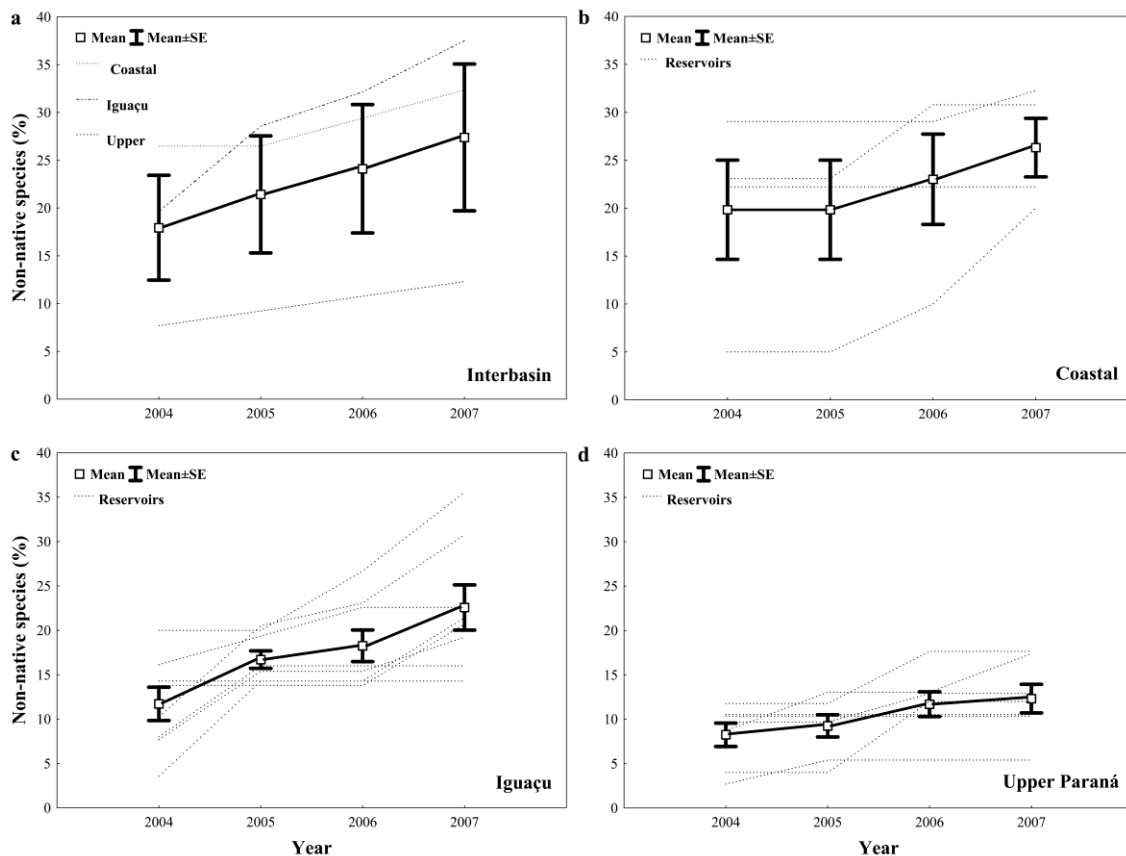
Fig. 3 Variation in the percentage of non-native species in the State of Paraná from 2004 to 2007, at the interbasin and intrabasin scales. The different dashed lines represent the variation interbasin. The *dotted lines* represent the variation intrabasin. The *bold line* and *open squares* represent the mean (±SE)

At the intrabasin scale, the metric Δ_J was negative for most of the pairwise comparisons of reservoirs within each basin, indicating that reservoirs within a basin had become more different. In the Coastal basin, the initial similarity of the assemblage was negatively associated with differentiation, and this association decreased over time, as indicated by the slopes of regression lines (Fig. 4). Geographically distant reservoirs became even more dissimilar than close reservoirs, but this association was significant only between the pristine assemblage and the assemblage sampled in 2007, indicated by the significance of a linear fit (P-2007, Fig. 4). In the Iguaçu basin, homogenization and/or differentiation could not be explained by either the similarity of the initial assemblage or geographical distance (Fig. 4). The Upper Paraná basin had a negative association between the initial similarity of the assemblage and Δ_J, indicating that the reservoirs had become more dissimilar. However, this association was significant only when the comparison was made between the pristine assemblage and assemblages sampled in 2005 and 2006 (Fig. 4). The comparison between the pristine assemblage and the assemblage

sampled in 2005 showed that distant reservoirs became more similar (i.e. homogenization), and differentiation occurred mainly between close reservoirs (Fig. 4).

Table 2 Frequency of occurrence of non-native species at the interbasin and intrabasin scales, and their vectors of introduction

Species	Vectors of introductions	Interbasin	Coastal	Iguaçu	Upper Paraná
Astyanax altiparanae	**Aquaculture**	0.650	**1.000**	**1.000**	
Brycon hilarii	Aquaculture	0.150	0.250	0.222	
Clarias gariepinus	Aquaculture	0.150		0.222	0.143
Ctenopharyngodon idella	Aquaculture	0.100		0.222	
Cyprinus carpio *	**Aquaculture**	**0.650**	**0.500**	**0.667**	**0.714**
Gymnotus inaequilabiatus	**Baiting**	0.350		**0.778**	
Gymnotus sylvius	**Baiting**	0.450		0.333	**0.857**
Hypophthalmichthys molitrix	Aquaculture	0.050		0.111	
Hypophthalmichthys nobilis	Aquaculture	0.100	0.250	0.111	
Ictalurus punctatus	Aquaculture	0.150	0.250	0.111	0.143
Leporinus friderici	Aquaculture	0.050		0.111	
Leporinus macrocephalus	Aquaculture	0.100		0.222	
Leporinus obtusidens	Aquaculture	0.100		0.222	
Leporinus octofasciatus	Aquaculture	0.050		0.111	
Leporinus piavussu	Aquaculture	0.050		0.111	
Micropterus salmoides *	**Sport fishing**	0.250	**1.000**		0.143
Odontesthes bonariensis	Stocking	0.200		0.444	
Oreochromis niloticus	**Aquaculture**	**0.600**	0.250	**0.556**	**0.857**
Plagioscion squamosissimus	Stocking	0.050			0.143
Prochilodus lineatus	Stocking	0.200	0.250	0.333	
Pseudoplatystoma corruscans	**Aquaculture**	0.100	**0.500**		
Pseudoplatystoma reticulatum	Aquaculture	0.050		0.111	
Salminus brasiliensis	Sport fishing	0.250	0.250	0.444	
Tilapia rendalli	**Aquaculture**	**0.800**	**1.000**	**0.778**	**0.714**

Bold values were referred to species that were found in more than 50% of the reservoirs. Non-native species considered within the ''100 worst invasive alien species'' list (Lowe et al., 2000) were marked with an asterisk. Species identification and vectors of introduction followed Oyakawa et al. (2006), Graça & Pavanelli (2007), and Baumgartner et al. (2012)

Interbasin

Coastal

Iguaçu

Upper Paraná

Fig. 4 Patterns of changes in assemblage similarity (Δ_J) as a function of the initial similarity of the assemblage and in relation the geographical distance of reservoirs, among assemblages of freshwater fish at the interbasin and intrabasin scales. The black lines separate biotic homogenization (positive Δ_J, values above zero) from biotic differentiation (negative Δ_J, values below zero). The *grayscale circles* and different dashes represent the different similarities/periods reported in the graphs (*black circle* P-2004, *dark gray circle* P-2005, *light gray circle* P-2006, and *white circle* P-2007). The values of slope and *P* of a linear fit was also showed in the graph

At the interbasin scale, and using the large spatial grain size, there was no relation between beta diversity and sampling period among basins (i.e. basins are not becoming similar) (Fig. 5). On the other hand, when the small spatial grain size was used, beta diversity decreased overtime (Fig. 5). Similarly, when we consider the intrabasin scale, the beta diversity decreased overtime for the Coastal and Upper Paraná basins. On the other hand, there was no relation between beta diversity and sampling period for the Iguaçu basin (Fig. 5). Seasonal variation on beta diversity was not found for any of the studied river basins (Fig. 5).

The total species richness and mean species richness were the most important variables explaining the variation in beta diversity using the large spatial grain size (Tables 3, 4). Similarly, using the small spatial grain size, in addition to these variables, all other variables were also relevant (Tables 3, 4). At the intrabasin scale, for the Coastal basin, total species richness and mean species richness per reservoirs were the most important variables explaining the beta diversity (Tables 3, 4). For the Iguaçu, introduction of non-native species was the most important mechanism for explaining the variation in beta diversity (Tables 3, 4). However, all other variables were also relevant. Finally, total species richness and mean species richness per reservoirs were, just as in the Coastal basin, the best variables to explain beta diversity in the Upper Paraná basin (Tables 3, 4).

Interbasin

Intrabasin

Fig. 5 Beta diversity among basins/reservoirs overtime at the interbasin and intrabasin scales. Pearson correlations, *P* values, and linear correlations (if significant) between beta diversity and sampling period (*Su* summer, *Au* autumn, *Wi* winter, *Sp* spring) were showed on the graphics. *N* indicates number of sampling units used to estimate beta diversity

Table 3 Model and number of parameters, values of Akaike information criterion adjusted (AIC$_c$), and difference between the model *i* and the best model (ΔAIC$_c$), for the best alternative models (i.e. ΔAIC$_c$ < 2.0) explaining beta diversity (β) trough different variables at the interbasin and intrabasin scales

Scales	Model	R^2	Number of parameters	AIC$_c$	ΔAIC$_c$
Interbasin					
Large spatial grain	$\beta \sim S + S_{avg}$	0.92	2	-124.82	0
	$\beta \sim S + S_{avg} + \%NN$	0.93	3	-123.74	1.09
	$\beta \sim S + S_{avg} + NN$	0.93	3	-123.65	1.17
Small spatial grain	$\beta \sim S + S_{avg} + NN$	0.63	3	-114.09	0
	$\beta \sim S_{avg} + \%NN$	0.51	2	-114.04	0.05
	$\beta \sim S + S_{avg} + \%NN$	0.61	3	-113.27	0.82
	$\beta \sim S_{avg} + Uniq$	0.48	2	-112.89	1.20
Intrabasin					
Coastal	$\beta \sim S$	0.25	1	-67.56	0
	$\beta \sim S + S_{avg}$	0.39	2	-67.24	0.32
Iguaçu	$\beta \sim NN$	0.31	1	-83.87	0
	$\beta \sim S + S_{avg}$	0.45	2	-83.80	0.06
	$\beta \sim S$	0.28	1	-83.25	0.61
	$\beta \sim \%NN$	0.24	1	-82.44	1.43
Upper Paraná	$\beta \sim \%NN + Uniq$	0.39	2	-82.10	1.76
	$\beta \sim S + S_{avg}$	0.57	2	-79.18	0

S species richness of the basins/reservoirs, *S$_{avg}$* mean species richness of basin/reservoir, *%NN* percentage of species that is nonnative, *NN* total number of non-native species, Uniq uniqueness (see ''Materials and methods'' section)

Table 4 The importance value of each variable according to multi-model inference, and the standard coefficient of each variable in multi-model inference for all alternative variables explaining beta diversity at the interbasin and intrabasin scales

Scales	Variables	Importance value	Standard Coefficient
Interbasin			
Large spatial grain	S	0.99	2.53
	S_{avg}	1.00	-2.28
	%NN	0.26	-0.11
	NN	0.27	-0.14
	Uniq	0.10	-0.15
Small spatial grain	S	0.45	0.82
	S_{avg}	0.85	-0.73
	%NN	0.41	-0.61
	NN	0.51	-0.27
	Uniq	0.24	0.35
Intrabasin			
Coastal	S	0.67	0.72
	S_{avg}	0.36	-0.47
	%NN	0.20	0.15
	NN	0.21	0.04
	Uniq	0.23	0.01
Iguaçu	S	0.47	0.64
	S_{avg}	0.36	-0.42
	%NN	0.31	0.40
	NN	0.43	0.54
	Uniq	0.25	0.25
Upper Paraná	S	0.89	1.34
	S_{avg}	0.97	-1.24
	%NN	0.20	-1.08
	NN	0.22	1.29
	Uniq	0.18	-1.71

S species richness of the basins/reservoirs, *S_{avg}* mean species richness of basin/reservoir, *%NN* percentage of species that is nonnative, *NN* total number of non-native species, Uniq uniqueness (see ''Materials and methods'' section)

Discussion

The major sources of introduced non-native species were through aquaculture (Pelicice et al., 2014), the aquarium industry (Gozlan, 2008; Magalhães & Vitule, 2013), and the intentional release of species for sport fishing, all without prior environmental impact assessments or subsequent monitoring, and indicative of poor enforcement of existing policies by the authorities (e.g. Cambray, 2003; Magalhães & Vitule, 2013). All vectors detected in the present study are a worldwide problem and, at least in part, a result of globalization (e.g. Cambray, 2003). In addition, non-native species are often better known or desired because of their recognized economic value than the relatively poorly studied local species (Cambray, 2003), and are therefore considered to be better suited for aquaculture, sport fishing, and fish stocking.

In freshwater ecosystems, the number of fish species introduced from different biogeographical zones has increased at the global scale (e.g. Welcomme, 1988; García-Berthou et al., 2005; Casal, 2006; Rahel, 2007; Vitule, 2009). The Neotropics has received the largest number of non-native species from other continents, and in this region, Brazil recorded a large number of introductions from other biogeographical zones (Agostinho & Júlio Jr., 1996). In addition, many species have been widely introduced from adjacent sub-basins (e.g. Agostinho et al., 2008; Vitule, 2009; Orsi & Britton, 2014). In our study, the proportion of non-native species at both the interbasin and intrabasin scales grew progressively from 2004 to 2007. This was especially true for the Iguaçu, in which there was an increase of 10 non-native species from 2004 to 2007.

Our study shows that aquaculture was the main vector of introduction for several non-native species. For example, *T. rendalli*, which was dominant in spatial terms (80% of the sampled reservoirs), was widely distributed in order to develop smallholder fish farming between 1950 and 1970 (Agostinho & Júlio Jr., 1996). It is also known to be an efficient invader of reservoirs (Ogutu-Ohwayo, 1990; McKaye et al., 1995; Pérez et al., 2003, 2004). Recently, in Brazil, a law has been proposed in the congress that would allow the rearing of non-native species for aquaculture (Pelicice et al., 2014). This activity can create an intensive and constant flow of non-native species into the ecosystem, since escapes are inevitable (Azevedo-Santos et al., 2011; Pelicice et al., 2014); the negative effects of these species are well documented (e.g. McKaye et al., 1995; Figueredo & Giani, 2005; Agostinho et al., 2007; Pelicice & Agostinho, 2009; Vitule et al., 2009; Cucherousset & Olden, 2011; Alexander et al., 2014; Pelicice et al., 2014). Other

introduced species detected in our study include *C. carpio* and *M. salmoides*, both listed among the ''100 worst invasive alien species'' (e.g. Lowe et al., 2000). *Cyprinus carpio* is one of the most widespread non-native species globally and *M. salmoides* was introduced into Brazil for sport fishing (Petesse &Petrere Jr., 2012). The introduction of species for sport fishing, mainly in reservoirs (Cambray, 2003; Clavero et al., 2013), is related to the growth of this sport worldwide and has resulted in an increase in the number of successful establishments because of the multiple introductions (e.g. Cambray, 2003; Lockwood et al., 2005; Britton & Orsi, 2012; Clavero et al., 2013).

Our data suggest that the effect of non-native species was to a large extent context dependent, since the major patterns of the homogenization and/or differentiation process differed among basins/reservoirs in the State of Paraná. The processes of biotic homogenization and/or differentiation caused by non-native species are dependent on spatial and temporal scales, and the differences in these processes will increase with increasing non-native richness and decrease with increasing native richness (Clavero & García-Berthou, 2006; Olden, 2006; Harris et al., 2011). The scales considered in this study were relevant with regard to outlining some unexplored patterns of biodiversity changes overtime and space in Neotropical reservoirs. The dynamics of homogenization and/or differentiation may influence local biodiversity, particularly through integrating local processes such as invasion and extirpation, which, in turn, may lead to large scale homogenization, and, over the long term, often reduces biodiversity in landscapes (e.g. Rahel, 2002; Olden & Rooney, 2006). The complexity of the temporal dynamics of the homogenization process in the Iberian Peninsula was investigated by Clavero & García-Berthou (2006). They differentiated the process into short and extended timescales, since, while fish assemblage homogenization was found in their large scale analysis, homogenization is a dynamic process, and finegrained temporal analyses detected some transient phases in the differentiation of the assemblage. This result provides evidence that the negative impacts of the invasion by a non-native species, in many instances, can have lag times, especially during the process of expansion into new areas and new settlements (e.g. Vitule et al., 2012; Simberloff & Vitule, 2014 and references therein).

In our study, we showed homogenization overtime at the interbasin scale, corroborating the results of several previous studies looking at changes in assemblage similarity and the homogenization of fish faunas around the world (e.g. Marchetti et al., 2001; Olden & Poff, 2004; Taylor, 2004; Clavero & García-Berthou, 2006). The homogenization pattern found in our study was created by both widespread introduction

of cosmopolitan species and the differential extirpation of native species. A common group of non-native species (i.e. a small number of the expanding non-native species, 'winners' according to McKinney & Lockwood, 1999), were repeatedly released into most of the reservoirs of the Coastal, Iguaçu, and Upper Paraná basins, and has become established in the major basins of the State of Paraná and in many regions around the world. The main introduced non-native species found in our study, *C. carpio*, *Ictalurus punctatus*, *M. salmoides*, *O. niloticus*, and *T. rendalli* include the most widespread introduced species worldwide. Moreover, these species have been associated with the homogenization of fish faunas in North America (Rahel, 2000, 2007), Iberian Peninsula (Clavero & García-Berthou, 2006; Clavero & Hermoso, 2011), and Brazil (Petesse & Petrere Jr., 2012; Vitule et al., 2012).

In contrast with the results observed at the interbasin scale, at the intrabasin scale we observed assemblage differentiation overtime, primarily in the Coastal and Upper Paraná basins. The decreased spatial scale allows differences in assemblage similarity between each pair of reservoirs to become more apparent (e.g. Marchetti et al., 2001; Olden & Poff, 2003; Clavero & García-Berthou, 2006), as has been reported by previous studies (e.g. Marchetti et al., 2001; Olden & Poff, 2004). In our study, the general pattern of differentiation was supported by different mechanisms in each reservoir, including the introduction of non-native species and/or the extirpation of riverine native species. Generally, the initial fish assemblages within each basin were believed to be more similar, i.e. assemblages within each basin were historically unique due to evolutionary isolation from other basins (e.g. Olden & Poff, 2004; Rahel, 2007). However, each reservoir within a basin has experienced its own history of introductions of different non-native species, especially introductions of species from adjacent sub-basins and reservoirs by different vectors, thereby causing biotic differentiation.

The pattern of differentiation found in the Coastal basin was indicated by the decreased similarity in the assemblages overtime among reservoirs. Changes found in each reservoir in relation to the initial assemblage were influenced by the extirpation of native species and by the introduction of different non-native species (e.g. predators), even when the non-native species were not necessarily established (e.g. because of the presence of a few large top predator or strong propagule/colonization pressure; Cunico & Vitule, 2014). In this basin, geographically distant reservoirs have tended to become more differentiated than close reservoirs. This pattern was probably related to the special circumstances related to the Capivari reservoir. This reservoir is not only the farthest from

the other reservoirs, but has the largest area and the largest number of recorded species, both native and non-native species, relative to the other reservoirs of this basin. Moreover, we can speculate that among the factors leading to this result are propagule pressure, urbanization, dendritic configuration of basins, hydrological connectivity, and the age of reservoirs. Indeed, some studies in Paraná State have reported that species richness is negatively correlated with the age of reservoirs (e.g. Agostinho et al., 1999; Gubiani et al., 2011). Thus, older reservoirs may have lower richness when compared to young reservoirs, because some species are not able to proliferate, leading to extirpation, thereby reducing species richness (Agostinho et al., 1999, 2008). Even more, overtime many non-native species can massively disrupt local assemblages (e.g. Pelicice & Agostinho, 2009; Pelicice et al., 2015).

For Iguaçu basin, we cannot conclude that non-native invasions were directly responsible for the observed homogenization and/or differentiation both in relation to similarity of the initial assemblages and to geographical distance among reservoirs. However, in this basin specifically, we found the largest number of non-native species, increasing from 11 in 2004 to 21 in 2007, indicating that the dispersion of these species can have negative effects on the native fish fauna, and must be better monitored and effectively controlled (e.g. Gubiani et al., 2010a; Daga & Gubiani, 2012). It appears that there were few cases of the same species being introduced into multiple reservoirs, which would lead to homogenization. However, there may be several cases of different non-native species being introduced in each reservoir or native species being extirpated in different reservoirs, leading to biotic differentiation. In fact, the processes proposed above are complex (Dar & Reshi, 2014 and references therein), making it hard to make predictions of long-term patterns for the basin.

Our study showed that the Iguaçu basin had both the largest numbers of endemic and non-native species, suggesting that the negative effects of non-native species should be most severe in this basin (e.g. Dextrase & Mandrak, 2006; Raghavan et al., 2008; Daga & Gubiani, 2012). Moreover, the Iguaçu basin has a long history of introductions of non-native species, with the impacts of establishment of the *C. carpio* already reported prior to the construction of the currently existing reservoirs in this basin (e.g. Myers, 1947). In the broader sense, invasions by non-native species are particularly important in the Iguaçu basin (Vitule, 2009; Espínola et al., 2010; Gubiani et al., 2010a), since this river is considered to be a unique and rare ecoregion with exclusive aquatic biodiversity (Abell et al., 2008; Pavanelli & Bifi, 2009). Even so, a cascade of reservoirs

containing non-native species may lead to an increased rate of invasion and negative effects on a landscape scale, since all of the reservoirs may have the appropriate conditions for the establishment of the non-native species (Johnson et al., 2008; Espı́nola et al., 2010). Also, we expect a high probability of positive interactions between non-natives with a real possibility of a future invasional meltdown (Simberloff &Von Holle, 1999).

The number of invasive non-native species is often directly related to presence of human activity and, particularly, to economic activities (e.g. McKinney, 2006; Leprieur et al., 2008). Generally, reservoirs located close to large urban centers have a higher probability of invasion (Espínola et al., 2010); several studies have reported positive correlations among the distribution of introduced fish species, human population density, urbanization, and infrastructure (e.g. Lockwood et al., 2005; McKinney, 2006). Therefore, the introduction of several non-native species may have played a large role in the differentiation at the intrabasin scale, because of their proximity to the large urban centers, such as the metropolitan region of Curitiba for Coastal basin and for the Foz do Areia reservoir in the Iguaçu basin as reported by Daga & Gubiani (2012). For the Iguaçu basin, the large nutrient input from the metropolitan region of Curitiba, which favors primary production, could contribute greatly to large numbers of non-native invasive fishes (Gubiani et al., 2008). The nutrient input can temporarily increase resource availability, thus creating opportunities for strong and tolerant non-native species (Havel et al., 2005). In addition, reservoirs close to urban centers are subject to large propagule pressure (Lockwood et al., 2005; Simberloff, 2009) from a wide range of non-native species released into the reservoirs, thereby increasing the likelihood of establishment, i.e. increasing the colonization pressure even more (see Lockwood et al., 2009).

The temporal differentiation observed in the Upper Paraná basin is possibly the result of multiple local and unexplored extirpation (Vitule et al., 2012), at least in the scales available here. This pattern may also be a consequence of the probable establishment of different non-native species in different reservoirs, for example, *I. punctatus* in the Rio dos Patos reservoir and *M. salmoides* in the Mourão reservoir. Moreover, the role of reservoirs in the decrease of fish populations in the Upper Paraná is well documented (Agostinho et al., 2007; Júlio Jr. et al., 2009; Espínola et al., 2010). In this basin, our results show that geographically close reservoirs became more different and distant reservoirs became more similar over time. This can be explained by its geological and hydrological division into sub-basins, and, more importantly by the

extirpation of different native species evident in the pairwise comparisons of distant reservoirs.

In addition to using changes in Jaccard's similarity index to evaluate homogenization and/or differentiation, we also evaluated beta diversity in the basins/reservoirs based on the dispersion of the reservoirs' scores in a multivariate space (see Anderson et al., 2011). In this case, the degree of homogenization is not evaluated by paired reservoirs, but by considering the entire basin in the landscape. In this approach, decrease in the beta diversity of the basin/reservoir overtime indicates that the overall similarity of the basins/reservoirs is increasing. However, it is important to note that the two approaches used here did not indicate the same result. Therefore, the beta diversity approach was applied with the primary purpose of investigating whether basins/reservoirs were becoming more homogenized over the period from 2004 to 2007, and what were the most probable causes of the changes in beta diversity (Olden & Poff, 2003). Worldwide assemblages are experiencing major biodiversity changes but not systematic biodiversity loss; in many cases, there is a rise in alpha diversity and a loss in beta diversity due to climate change and species invasions (Dornelas et al., 2014).

Our results indicate that the mechanisms explaining beta diversity in the studied basins/reservoirs differed over space and time. At the interbasin scale, the decrease in beta diversity was better explained by a decrease in species richness. Moreover, at the small spatial grain, the introduction of non-native species was responsible for promoting homogenization, primarily by the introduction of the same species in most of the reservoirs. On the other hand, at the intrabasin scale, the Coastal and Upper Paraná basins, the decrease in beta diversity was better explained by a decrease in species richness. Modified ecosystems can impoverish assemblages of native species (Clavero et al., 2013). For example, reservoirs tend to homogenize environmental conditions (Agostinho et al., 2007; Petesse & Petrere Jr., 2012), so that species occurring in restricted habitats may either spread or be extirpated, thereby causing homogenization (Lockwood et al., 2007; Rahel, 2007). For the Iguaçu basin, the introduction of non-native species was the most important mechanism explaining variation in beta diversity. However, the variation beta diversity was generally explained in terms of the landscape and did not show a decrease overtime. Similarly, Hermoso et al. (2012) has found that the abundance of introduced species was the most important factor explaining the homogenization processes in native assemblages in Guadiana River basin. Thus, our results suggest that high richness of non-native species and differential propagule

pressure or even colonization pressure in the reservoirs of Iguaçu may, at least partially, explain beta diversity in this basin. In this sense, a large faunal similarity between regions suggests that they are losing their biological specificity. The homogenization of assemblages within a given region suggests a loss of ecological complexity, which is the main component of biodiversity (Lambdon et al., 2008) and of ecosystem function (e.g. Dirzo et al., 2014).

Finally, we highlight the fact that while the consequences of globalization, including environmental modifications and the introductions of non-native species, can often increase local biodiversity, at a landscape or global scale they lead to a major loss of aquatic biodiversity. Therefore, the process of homogenization and/or differentiation can continue long after the initial construction of the dam, demonstrating that the impacts of dams are irreversible, and their consequences can have strong long-term effects (e.g. Petesse & Petrere Jr., 2012; Vitule et al., 2012). Moreover, habitat disturbances, such as the increase of connectivity in aquatic environments, may promote favorable environmental conditions for non-native species, allowing them to become established more easily (e.g. D'Antonio & Meyerson, 2002; McKinney, 2006; Woodford et al.,2013), and thus, facilitate the biotic homogenization, especially because reservoirs act as stepping stones for invaders, easing the spread of introduced species and the establishment of new populations (Havel et al., 2005; Vitule et al., 2012). Furthermore, human-mediated introductions in aquatic ecosystems occur for several reasons, including the aquarium industry, sport fishing, and fish farming (Magalhães & Vitule, 2013; Pelicice et al., 2014). This is a troubling issue that urgently needs the development of management strategies, especially since these activities are being encouraged and stimulated in developing countries such as Brazil (Pelicice et al., 2014). Once introduced, non-native species tend to spread either by natural means, through sport fishing and fish farming, or by new construction of dams and waterways (Cambray, 2003).

Conclusions

Our study emphasizes the value and utility of the lists of species and other basic ecological information generated by basic investigations and fisheries monitoring programs; this information is generally poorly used in developing and mega-diverse countries. In particular, we demonstrated and quantified the process of biotic homogenization and/or differentiation over time and space in Neotropical reservoirs using such data. In our study, these processes were driven primarily by the introduction of non-native species through aquaculture. Moreover, we emphasize the importance of spatial scale in the perception of the processes of homogenization and/or differentiation, since we detected biotic homogenization occurring at the interbasin scale, whereas the biotic differentiation was observed at the intrabasin scale. Furthermore, our results indicate that beta diversity decreased over space and time for the studied basins/reservoirs, suggesting that fish assemblages are becoming even more homogenized overtime. The mechanisms underlying the decrease in beta diversity and their dynamics differed among basins/reservoirs studied.

The development of a variety of indicators to quantify biotic homogenization and/or differentiation is necessary if we are to measure and understand the changes in turnover rates and the number of species. Furthermore, we highlight the need for more long-term studies of the impacts of non-native species and the dynamics of homogenization, especially in areas of high species richness and endemism, where the conservation of biodiversity is a major challenge. It is our hope that future invasions will be prevented, or at least be controlled more effectively.

Reservoirs and introduction of non-native species determine the taxonomic and functional homogenization patterns of freshwater fish assemblages in the State of Paraná, Brazil

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ABSTRACT

Aim Human activities have intensified the habitat modification and non-native species introductions. These activities combined with extirpation of native species, have caused severe changes in species composition and at the diversity of biological traits of fishes around the world. Here, we assessed the temporal and spatial changes in both taxonomic and functional similarities of freshwater fishes in Neotropical reservoirs.

Location Southern Brazil.

Methods The taxonomic and functional similarities of the fish fauna among reservoirs were quantified at inter-ecoregion and intra-ecoregion scales, to assess the dynamics of the homogenization or differentiation over the period 2002-2007. Moreover, the temporal variation in the dispersion of functional traits composition of the initial, native, native extirpated and non-native assemblages was calculated.

Results At the inter-ecoregion scale, the taxonomic similarity increased over time, whereas the functional similarity decreased in the early years of study (functional differentiation), but increased in the last period (functional homogenization). At the intra-ecoregion scale, most ecoregions showed a decrease in taxonomic and functional similarities over time, except the Iguaçu ecoregion, in which the functional similarity increased over time. When comparing initial, native and native extirpated assemblages with non-native assemblages, the last shared the functional space with native extirpated at inter-ecoregion scale (i.e. non-native species replaced native species functionally similar). Whereas at intra-ecoregion scale most of non-native species (large-bodied and great-weight species, possessing omnivore and piscivore feeding habitats) have not shared the functional space with native extirpated species.

Main conclusions Patterns of the changes in the taxonomic and functional composition of freshwater fish fauna were dependent on the spatial and temporal scale. Moreover, our results reinforced that different transition phases can occur in the dynamics of the biotic homogenization phenomenon. In addition, we emphasize the need for further conservation attention and understanding of the changes in the functional diversity of freshwater fishes, which are under severe anthropogenic pressure in the Neotropics.

Keywords

biodiversity change, functional diversity, dams, taxonomic differentiation, trophic guild.

INTRODUCTION

The anthropogenic pressures in most ecosystems worldwide, in the past and ongoing, are consequence of activities related to urbanization (McKinney, 2006), human population growth (Olden *et al*., 2006a; Lockwood *et al*., 2007), fast and abrupt elimination of biogeographic barriers (Rahel, 2007; Vitule *et al*., 2012), land-use intensification and habitat loss (Vitousek *et al*., 1997). These human activities have changed the distribution of species globally, and not only facilitating but accelerating the massive introduction and establishment of widespread non-native species (Leprieur *et al*., 2008; Wilson *et al*., 2009; Seebens *et al*., 2017). These alterations on the natural patterns of distinctiveness in biotas, have been causing the biotic homogenization process (McKinney & Lockwood, 1999; Olden *et al*., 2004; Hermoso *et al*., 2012), which has promoted the global exchange of species and increased the uniformity of biotas across all zoogeographic regions and taxonomic groups (Lövei, 1997; Olden *et al*., 2006a; Villéger *et al*., 2011; Baiser *et al*., 2012). As result, there are many novel and underexplored threats to biodiversity (Olden *et al*., 2010) and impacts to the ecosystem services (Vilá *et al*., 2010).

The biotic homogenization process often encompasses taxonomic, functional and genetic simplification of biotas (Smart *et al*., 2006; Baiser & Lockwood, 2011; Pool & Olden, 2012). However, of the different types of biotic homogenization (Olden *et al*., 2004; Winter *et al*., 2009), the taxonomic homogenization has received more attention, mainly evaluating freshwater fish around the world (Rahel, 2000; Clavero & García-Berthou, 2006; Menezes *et al*., 2015; Toussaint *et al*., 2014, 2016a). On the other hand, a smaller number of studies have quantified the functional homogenization, generally assessing large spatial and/or temporal scales (Winter *et al*., 2008; Clavero & Brotons, 2010; Marr *et al*., 2013). Although these concerns have increased the interest and research effort in quantifying the homogenization patterns, there remains considerable uncertainty in our understanding related to the dynamics of this process (Olden, 2006; Olden *et al*., 2010). Moreover, up to the present time, research effort has predominantly focused in developed countries from temperate region (Rahel, 2000; Baiser *et al*., 2012; Villéger *et al*., 2014), normally considering changes in species composition at a single spatial scale (e.g. Winter *et al*., 2009; Olden *et al*., 2016).

In such context, beside the increasing advances related to the homogenization of freshwater fish during the last decade (e.g. Petsch, 2016), some critical gaps in the

knowledge still remains, particularly due to the scale-dependent patterns and the determinant mechanisms of this process. Although much of the literature have extensively studied only one of the three forms of homogenization: the taxonomic homogenization, it is now conceivable that freshwater fish assemblages may have lost even more diversity in terms of functional composition (e.g. Pool & Olden, 2012; Buisson *et al.*, 2013; Villéger *et al.*, 2014). This fact is a growing concern, especially in zoogeographic regions considered hotspots of functional diversity, such as the Neotropics, region with the highest functional richness of freshwater fishes (Toussaint *et al.*, 2016b). Moreover, this region is already under severe threat and facing the loss of diverse fish species, resulting in greater losses in the functional diversity when compared to taxonomic diversity (e.g. Vitule *et al.*, 2016, 2017).

In addition, freshwater systems in the Neotropics have been severly impacted, with river damming being one of the most widely distributed alterations (e.g. Agostinho *et al.*, 2008; Lehner *et al.*, 2011; Winemiller *et al.*, 2016). The construction of dams can result in the elimination of natural barriers to fish dispersal (Julio Jr. *et al.*, 2009; Vitule *et al.*, 2012; Casimiro *et al.*, 2017), fragmentation of the fluvial habitats (Nilsson *et al.*, 2005), promote the homogenization of the natural flows regimes of rivers (Moyle & Mount, 2007; Poff *et al.*, 2007), cause changes in the composition and abundance of species (Agostinho *et al.*, 2016), and lead to the taxonomic homogenization of fish assemblages (Clavero & Hermoso, 2011; Vitule *et al.*, 2012; Petesse & Petrere Jr, 2012). Moreover, the physical and hydrological alterations imposed by the construction of dams can facilitate the introduction and establishment of non-native adapted species, which have displaced native fishes at a global scale (Havel *et al.*, 2005; Johnson *et al.*, 2008; Caiola *et al.*, 2014; Liew *et al.*, 2016), degrading fisheries and ecosystem services (e.g. Hoeinghaus *et al.*, 2009; Olden *et al.*, 2014).

Therefore, the freshwater fish fauna in megadiverse developing countries located in this region possess the probability of even greater damage, due to the several proposed dams (Finer & Jenkins, 2012; Winemiller *et al.*, 2016), land degradation (e.g. Roa-Fuentes & Casatti, 2017), aquaculture practices and introduction of non-native species (Agostinho & Julio Jr., 1996; Pelicice *et al.*, 2015; Daga *et al.*, 2016; Frehse *et al.*, 2016). In addition, current research regarding the freshwater fish have focused on dynamics of the taxonomic homogenization process in reservoirs of this megadiverse region (Petesse & Petrere Jr., 2012; Vitule *et al.*, 2012; Daga *et al.*, 2015), while the functional homogenization deserves additional greater attention and quantification,

mainly due to this form of homogenization possess significant implications for community and ecosystem functions (e.g. Olden, 2006). Thus, in order to go beyond of the quantification of taxonomic homogenization and provide a better insight of the patterns of functional homogenization, the present study used a set of biological and ecological traits, aiming to quantify the extent and the dynamics of the temporal changes in taxonomic and functional similarities of freshwater fish assemblages across Neotropical reservoirs, at two different spatial scales: *i*) at inter-ecoregion scale: evaluating the changes in taxonomic and functional similarities considering all reservoirs of the three ecoregions; and, *ii*) at intra-ecoregion scale: assessing the changes in taxonomic and functional similarities considering the reservoirs within each individual ecoregion. In addition, the main traits that contributed to the changes in the functional similarity of native, native extirpated and non-native freshwater fish assemblages were identified.

METHODS

Study area and fish sampling

Twenty reservoirs were sampled, which are located in three major freshwater ecoregions (Abell *et al*., 2008) in the Southern Brazil: the Southeastern Mata Atlantica, Iguaçu and Upper Paraná ecoregions (Fig. 1).
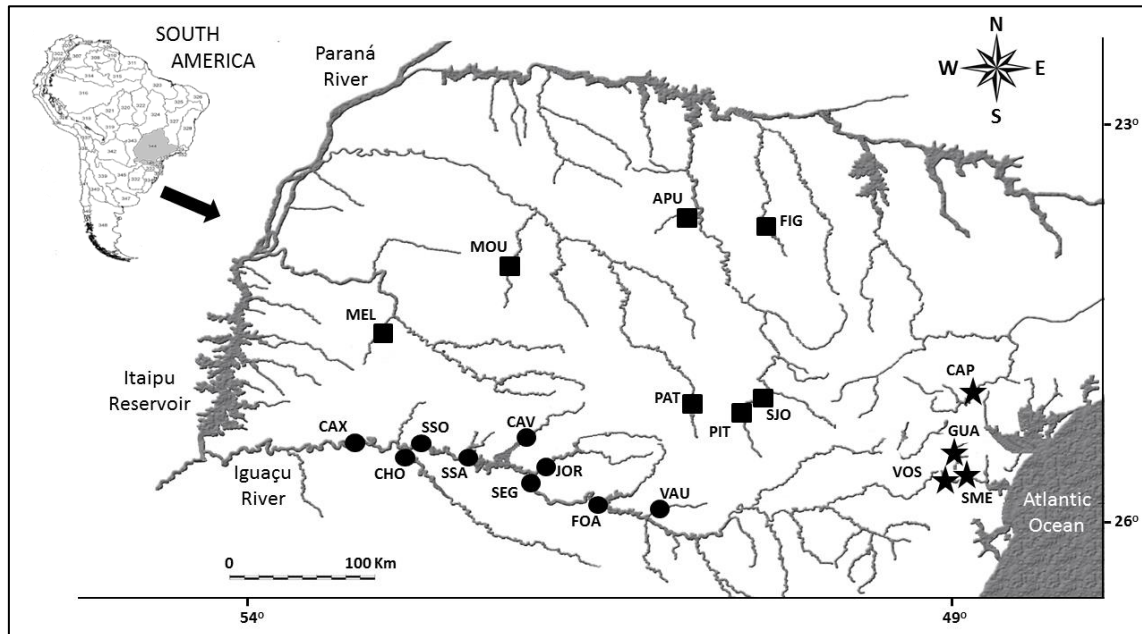
Figure 1 Location of the 20 reservoirs in three major freshwater ecoregions in the State of Paraná, Southern Brazil (ecoregions codes: 331, 344 and 346 according to Abell *et al*., 2008). The different symbols represent the ecoregions (*black stars* Southeastern Mata Atlantica, *black circles* Iguaçu, and *black squares* Upper Paraná).

The Southeastern Mata Atlantica ecoregion includes all of the coastal drainage basins, encompassing a drainage area of 14,674 Km^2 (Maack, 2012). The Iguaçu ecoregion includes the Iguaçu river and all the tributaries from its headwaters in the metropolitan region of Curitiba to Iguaçu Falls, with a drainage area of 72,000 Km^2 (Maack, 2012; Daga *et al*., 2016). The Upper Paraná ecoregion includes the drainage basin of the upper Rio Paraná and its tributaries above the former Guaíra Falls, the Piquiri, Ivaí and Tibagi rivers, encompassing a drainage area of 186,321 km^2 (Maack, 2012; Daga *et al*., 2016). We considered four reservoirs for the Southeastern Mata Atlantica ecoregion, nine for the Iguaçu ecoregion and seven for the Upper Paraná ecoregion (Table 1).

Table 1 Characteristics of the 20 reservoirs sampled

Ecoregion	Reservoir	Year of closure	Area (km²)	Depth (m)	Transparency (m)	Mode of operation
Southeastern Mata Atlantica	Capivari	1970	12.0	43	2.4	Overflow
	Guaricana	1957	7.0	17	1.9	Overflow
	Salto do Meio	1949	0.1	6.2	1.4	Run-of-the-river
	Vossoroca	1949	5.1	13	2.6	Overflow
Iguaçu	Cavernoso	1950	2.9	8	0.9	Run-of-the-river
	Chopim I	1965	2.9	6	0.6	Run-of-the-river
	Derivação do Jordão	1996	3.4	60	1.2	Run-of-the-river
	Foz do Areia	1980	139.0	135	1.4	Overflow
	Salto Caxias	1998	124.0	53	2.5	Run-of-the-river
	Salto Osório	1975	55.0	40	2.7	Run-of-the-river
	Salto Santiago	1979	208.0	70	2.0	Overflow
	Salto do Vau	1959	2.0	4	1.8	Run-of-the-river
	Segredo	1992	82.4	100	1.3	Overflow
Upper Paraná	Apucaraninha	1958	2.0	13	0.6	Run-of-the-river
	Figueira	1963	< 1.0	-	-	Run-of-the-river
	Melissa	1962	2.9	5	0.2	Run-of-the-river
	Mourão	1964	11.3	13	1.7	Overflow
	Pitangui	1911	0.2	-	-	Run-of-the-river
	Rio dos Patos	1949	1.3	6	0.4	Run-of-the-river
	São Jorge	1945	7.2	-	-	Overflow

Data compiled from Júlio Jr. *et al*. (2005), Agostinho *et al*. (2007), Espínola *et al*. (2010), and Gubiani *et al*. (2012).

The fish assemblages were sampled from May 2002 to December 2007, covering a six-year period. The sampled data were summarized according to the following time periods: 2002/2003, 2004/2005 and 2006/2007. To the 2002/2003 period the sampling was non-standardized, while to the 2004/2005 and 2006/2007 periods the effort was standardized for all reservoirs, by using only the data recorded in four months per year (i.e. corresponding to one month per season).

Fish were captured using a set of gillnets (mesh size: 2.4 to 16 cm between opposite knots) and trammel nets (mesh size: 6 to 8 cm); which contained 10 to 20 m in lenght and 1.5 to 4.5 m in height. In most of the reservoirs, the set of gillnets were operated in three sampling sites arranged along the reservoirs; while in Salto Santiago and Salto Osório reservoirs the gillnets were operated in five and four sampling sites respectively. The set of gillnets were operated in the surface, bottom and margin of each sampling site

and exposed for 24 hours. In addition, in the littoral areas of the reservoirs, the fish were captured with a 20 m long seine net (0.5 cm mesh size), during the day and night periods.

After sampling, the fish were anesthetized with benzocaine hydrochloride solution (250 mg/l), as recommended by AVMA (2001). The species identification was based on a specialized bibliography (Ingenito *et al*., 2004; Oyakawa *et al*., 2006; Graça & Pavanelli, 2007; Menezes *et al*., 2007; Baumgartner *et al*., 2012). Moreover, for all individuals we measured: total length, standard length, total weight, gonad weight, and determined the sex and gonad development stages (following Vazzoler, 1996). For most fish species, the trophic guild was determined based on the analysis of stomachs contents, seeking to identify the predominant food items in the diet and feeding habits of fishes into the real ecosystem sampled. However, for some fishes the stomach contents were not examined, and then the trophic guild was obtained from literature (Table S1 in Supplementary Material – Appendix 7).

Datasets of freshwater fish

The datasets were constructed based on sampling data from all reservoirs occurences for each time period: initial (which was considered to be representative of the 'original' pool of species, corresponding only to native species recorded in 2002/2003) and current (fish records to each period: 2002/2003, 2004/2005 and 2006/2007, consisting of native and non-native species). Native species corresponded to indigenous species occurring in each ecoregion as result of natural processes, while native extirpated species were those present in the initial dataset but absent at the dataset of the later periods. Non-native species were considered as those that had established reproducing populations, as result of the species translocations (extralimital introductions from other ecoregions within the Neotropical region) or introduction of foreign species (extraregional introductions from other zoogeographic regions), and with some local or regional scatter in distribution (e.g. Blackburn *et al*., 2011). Thus, our datasets accounted for the status of each species (native, native extirpated and non-native) in each reservoir, which allowed us to evaluate the changes in the initial and current species composition and functional attributes, representing the invasion-extinction scenario proposed by Olden & Poff (2003).

In order to quantify the extent of the changes in functional trait composition, life-history and ecological traits were used from collected data and literature (Table 2). The general life-history and ecological traits obtained from sampled dataset were:

standard body length, total weight, gonad development stages, gonad weight and trophic guild. This last trait was also complemented with the literature information when needed. Moreover, some traits were calculated with base in field dataset: sexual ratio, gonadosomatic index (GSI), total length-standard length relationship (LT/LS relationship) and length-weight relationship (LWR). The other traits were compiled from literature and FishBase (http://www.fishbase.org/) (Froese & Pauly, 2016): mouth position, trophic level and water column position. As the trait assignments were categorical or continuous, the mean value and standard deviation for each continuous trait or frequency of each categorical trait were included, for each trait per local or regional assemblages.

Table 2 List of life-history and ecological traits used to describe the fish functional composition

Functional trait	Type	Range / Categories	Description	Interpretation	Information source
Body length	Continuous	2.3 - 93.0 cm	The standard body length (distance between the snout and the last vertebra; cm)	Related with growth rate, which is associated with mortality rates, longevity and reproductive output	Collected data
Total weight	Continuous	0.3 - 29975.0 g	Total weight of each individual in grams	Related to the health of an individual or group of fish, and associated to the growth and reproduction	Collected data
Gonad development stages	Continuous	0 - 1	Calculated as the ratio of each gonad development stage and the humber of individuals of each species	Suggests information about the reproductive biology of fish species	Collected data
Gonad weight	Continuous	0.01 - 10481.9 g	The gonad weight of each individual in grams	Related to the relative gonadal development or activity	Collected data
Trophic guild	Categorical	Detritivore Herbivore Omnivore Piscivore Invertivore Insetivore Planktivore	Analysis of the stomach contents	Preferred food items and feeding habits	Collected data and literature
Sexual ratio	Continuous	0.3 - 55.5	Calculated as the ratio between the number of adult females and males	Demographic parameter correlated to the population growth and mortality	Collected data

rates, inbreeding and competition for mates

Gonadosomatic index (GSI)	Continuous	0.01 - 44.6	(GSI = gonad mass / total body mass × 100)	Estimator of reproductive condition	Collected data
Total length-standard length relationship (LT/LS relationship)	Continuous	0.4 - 24.0 cm	Calculated as the relationship between total length minus the standard length	Caudal fin aspect ratio	Collected data
Length-weight relationship (LWR)	Categorical	Isometric growth (b = 3.0) Positive allometry growth (b > 3.0) Negative allometry growth (b < 3.0)	Total weight = $a\mathrm{SL}^b$ (SL= standard length) Average b-value (slope)	Estimation of the condition or 'well being' of the fish	Collected data
Mouth position	Categorical	Inferior (ventral) Subterminal Terminal Superior	Position of the fish's mouth	Suggest in which part of the habitat the fish acquires its food	Literature
Trophic level	Continuous	2.0 - 4.5	Obtained from food items records using the TROPH subroutine (available in FishBase)	Related to the trophic position	Literature
Water column position	Categorical	Demersal Benthopelagic Pelagic	Fish position in the water column	Related to the habitat use	Literature

Statistical analysis

Data were analyzed at two different spatial scales. First, at the inter-ecoregion scale, in which the 20 reservoirs of the three major sampled ecoregions were considered. Second, at the intra-ecoregion scale, in which the reservoirs within each individual ecoregion were considered, i.e., four, nine and seven reservoirs for Southeastern Mata Atlantica, Iguaçu and Upper Paraná ecoregions respectively.

The species presence/absence data were considered to quantify the taxonomic homogenization process. For that, reservoir-by-species matrices were created separately for both inter-ecoregion and intra-ecoregion scales, which were converted into similarity matrices using Jaccard's coefficient (Olde & Poff, 2003; Olden & Rooney, 2006). This coefficient varies from 0 to 1, corresponding to no similarity and complete similarity, respectively (Olden & Poff, 2003). Thus, taxonomic similarity (*TS*) matrices were calculated separately for the initial assemblage (*TS* $_{initial}$) and for the assemblages sampled in each current period from 2002/2003 to 2006/2007 (*TS* $_{2002/2003}$, *TS* $_{2004/2005}$, *TS* $_{2006/2007}$), for both inter-ecoregion and intra-ecoregion scales (Figure S1 in Supplementary Material – Appendix 7).

To quantify the functional homogenization, an index of functional composition was computed, the community-level weighted means of trait values (hereafter CWM) (Lavorel *et al*., 2008). The CWM reservoir-by-trait matrices for inter-ecoregion and intra-ecoregion scales were created, by multiplying the reservoir-by-species matrix and species-by-trait matrix for each time period (e.g. Baiser & Lockwood, 2011; Pool & Olden, 2012). The CWM matrices represented the relative proportion of species in each reservoir exhibiting each trait state (Pool & Olden, 2012). The CWM matrices were converted into similarity matrices using Gower's distance (Villéger *et al*., 2014; Su *et al*., 2015). Then, the functional similarity (*FS*) matrices were calculated separately for the initial assemblage (*FS* $_{hist}$) and assemblages sampled in each current period from 2002/2003 to 2006/2007 (*FS* $_{2002/2003}$, *FS* $_{2004/2005}$, *FS* $_{2006/2007}$), for both inter-ecoregion and intra-ecoregion (Figure S1 in Supplementary Material – Appendix 7).

Changes in pairwise taxonomic and functional similarities were calculated between reservoirs at inter-ecoregion (considering only the reservoirs from different ecoregions) and intra-ecoregion scales for each time period, and measured as current similarities of a pair of reservoirs minus initial similarity of the same pair of reservoirs (for example: $\Delta TS = TS\,^{2002/2003}_{2006/2007}$ - $TS_{initial}$ and, $\Delta FS = FS\,^{2002/2003}_{2006/2007}$ - $FS_{initial}$) (Baiser &

Lockwood, 2011; Pool & Olden, 2012). Moreover, we also compared current situations (for example: $\Delta TS = TS\,_{2006/2007}^{2004/2005} - TS\,_{2004/2005}^{2002/2003}$ and, $\Delta FS = FS\,_{2006/2007}^{2004/2005} - FS\,_{2004/2005}^{2002/2003}$) (Clavero & García-Berthou, 2006) (Figure S1 in Supplementary Material – Appendix 7). A positive value indicated an increase in the similarity (i.e. homogenization), whereas a negative value indicated a decrease in the similarity (i.e. differentiation) (Olden & Poff, 2003; Olden & Rooney, 2006).

In addition, based on the CWM reservoir-by-trait distance matrices for inter-ecoregion and intra-ecoregion scales for each time period, the variation in the dispersion of the functional traits was estimated by the average distance of each initial, native, native extirpated and non-native assemblages traits composition, to their group centroid in an ordination space based on the dissimilarity matrices. For that, a Principal Coordinates Analysis (PCoA) was used (Legendre & Legendre, 1998), applied to the Gower dissimilarity matrices. In all current time periods for inter-ecoregion and intra-ecoregion scales, the first two principal axes of the PCoA explained the most of traits variation and were retained for interpretation (based on the Broken-Stick rule; Legendre & Legendre, 1998). Moreover, we calculated the Pearson's r correlations between the scores of the first two principal axes of the PCoA and the functional composition (i.e. with the CWM reservoir-by-trait matrices), for inter-ecoregion and intra-ecoregion scales in each current time period. Were considered values of Pearson's r correlations ≥ 0.70, and if $P < 0.05$ the correlations were statistically significant.

All the analyses were conducted in R software (R Development Core Team, 2008), under the packages: FD (Laliberté *et al.*, 2014) and vegan (Oksanen *et al.*, 2013) (Supplementary Material – Appendix 8). Jaccard and Gower similarity matrices were used for estimations of the changes in taxonomic and functional similarities, by calculating 1 minus the dissimilarity matrix provided in "vegdist" function. Values were considered significant when type I error was lower than 5%.

RESULTS

The reservoirs considered in this study hosted 96 native fish species. Among these, 38 were endemic to their respective ecoregions, being 24 endemic species to the Iguaçu ecoregion. Related to the native extirpated species, 11 species were considered extirpated. The Upper Paraná ecoregion had the highest number of both native and native extirpated species (54 and 7 species, respectively). Seven non-native species were considered to have been originated from other zoogeographical regions (e.g. Afrotropical, Nearctic and Palearctic regions), and nine non-native species were translocated from extralimital ecoregions (Table S2 in Supplementary Material – Appendix 7). The Iguaçu ecoregion had the highest number of non-native species (Table S2 in Supplementary Material – Appendix 7).

The inter-ecoregion and intra-ecoregion scales showed a opposite pattern related to the dynamic of the changes in the taxonomic similarities among reservoirs during the study time period. At the inter-ecoregion scale, the changes in mean taxonomic similarity among reservoirs increased over time, from 3.2% in 2002/2003 to 4.8% in 2006/2007 (Fig. 2a). At the intra-ecoregion scale, the changes in taxonomic similarity decreased; and, this decrease in similarity was higher in the first time period of study, indicating a general tendency towards taxonomic differentiation, with the exception of the Upper Paraná ecoregion in 2006/2007 (Fig. 2b, c, and d). To the Southeastern Mata Atlantica ecoregion, the changes in mean taxonomic similarity ranged from -6.3% in 2002/2003 to -0.1% in 2006/2007 (Fig. 2b). For the Iguaçu ecoregion, the changes in mean taxonomic similarity ranged from -6.7% in 2002/2003 to -2.2% in 2006/2007 (Fig. 2c). By the other hand, to the Upper Paraná ecoregion, the changes in mean taxonomic similarity ranged from -3.6% in 2002/2003 to 1.1% in 2006/2007 (Fig. 2d).
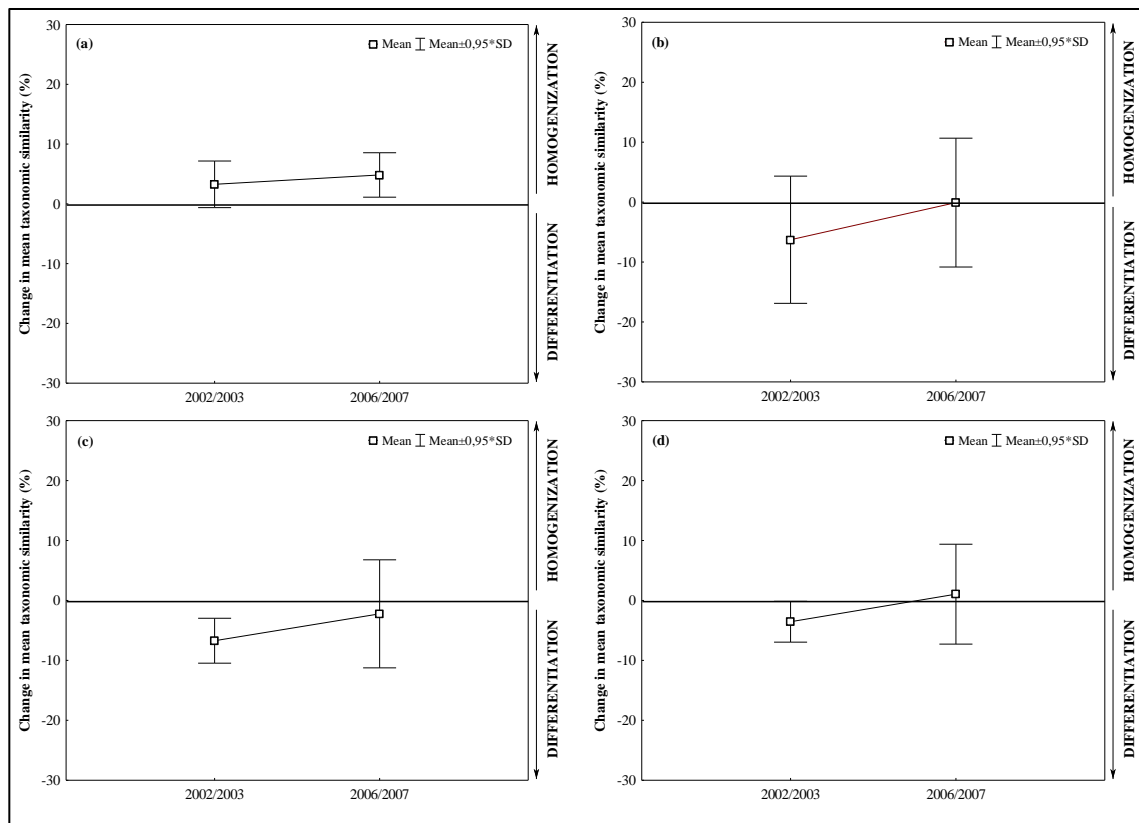
Figure 2 Mean changes in taxonomic similarity among reservoirs at inter-ecoregion and intra-ecoregion scales, for each time period. (a) Inter-ecoregion scale, (b) Southeastern Mata Atlantica, (c) Iguaçu, and (d) Upper Paraná ecoregions. Positive values represented taxonomic homogenization and negative values represented taxonomic differentiation.

At the inter-ecoregion scale, the majority of the changes in taxonomic similarity among pairs of reservoirs from the initial to the current periods were positive (92 out of 127 comparisons between initial and 2002/2003 period, and 117 out of 127 comparisons between initial and 2006/2007 period), indicating strong evidence of on-going taxonomic homogenization (Fig. 3a and b; Table S3 in Supplementary Material – Appendix 7). However, the changes in taxonomic similarity among pairs of reservoirs in the current situations were positive (90 out of 127 comparisons between 2002/2003 and 2004/2005 periods) (Fig. 3c) and negative (73 out of 127 comparisons between 2004/2005 and 2006/2007 periods), indicating that the addition of two new non-native species in the 2006/2007 period resulted in a decrease in taxonomic similarity (i.e. differentiation) (Fig. 3d) (Table S3 in Supplementary Material – Appendix 7).

Figure 3 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the inter-ecoregion scale (*n* = 127). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similaritiesy in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

On the contrary, at the intra-ecoregion scale, the changes in taxonomic similarity were negative for most of the pairwise comparisons, indicating that reservoirs of each ecoregion had become more different (i.e. taxonomic differentiation) (Table S3 in Supplementary Material – Appendix 7). To the Southeastern Mata Atlantica ecoregion, the majority of the changes in taxonomic similarity among pairs of reservoirs from the initial to the current periods were negative, indicating taxonomic differentiation (Fig. 4a and b; Table S3 in Supplementary Material – Appendix 7). However, the changes in taxonomic similarity among pairs of reservoirs in the current situations were both positive and negative, indicating that the addition of two new non-native species in both 2004/2005 and 2006/2007 periods resulted in a increase in taxonomic similarity (i.e. homogenization) (Fig. 3c and d) (Table S3 in Supplementary Material – Appendix 7).

Figure 4 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the Southeastern Mata Atlantica ecoregion ($n = 6$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

To the Iguaçu ecoregion, the majority of the changes in taxonomic similarity among pairs of reservoirs from the initial to the current periods were negative, indicating taxonomic differentiation (Fig. 5a and b; Table S3 in Supplementary Material – Appendix 7). However, the changes in taxonomic similarity among pairs of reservoirs in the current situations were positive (30 out of 36 comparisons between 2002/2003 and 2004/2005 periods, and 20 out of 36 comparisons between 2004/2005 and 2006/2007 periods), indicating that the addition of three new non-native species in the two last periods resulted in a wide range of responses, including the increase in taxonomic similarity (i.e. homogenization) in 2004/2005 (Fig. 5c), and the decrease in taxonomic similarity (i.e. differentiation) in 2006/2007 (Fig. 5d) (Table S3 in Supplementary Material – Appendix 7).

Figure 5 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the Iguaçu ecoregion (*n* = 36). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

To the Upper Paraná ecoregion, the majority of the changes in taxonomic similarity among pairs of reservoirs from the initial to the 2002/2003 period were negative (19 out of 21 comparisons), indicating taxonomic differentiation (Fig. 6a; Table S3 in Supplementary Material – Appendix 7). By the other hand, changes in taxonomic similarity among pairs of reservoirs from the initial to the 2006/2007 period were positive (13 out of 21 comparisons), indicating taxonomic homogenization (Fig. 6b; Table S3 in Supplementary Material – Appendix 7). Moreover, the changes in taxonomic similarity among pairs of reservoirs in the current situations were positive (13 out of 21 comparisons between both 2002/2003-2004/2005, and 2004/2005-2006/2007 periods), indicating that the addition of five non-native species over all the time periods analyzed, resulted in a

increase in taxonomic similarity (i.e. homogenization) (Fig. 6c and d) (Table S3 in Supplementary Material – Appendix 7).

Figure 6 Current periods versus initial taxonomic similarity for pairwise comparisons among reservoirs at the Upper Paraná ecoregion ($n = 21$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which taxonomic similarity has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which taxonomic similarity has decreased with time (i.e. taxonomic differentiation). Jaccard coefficient values are expressed as percentages.

Related to the dynamic of the changes in the functional similarities among reservoirs during the study time period, the inter-ecoregion and intra-ecoregion scales maintained the opposite general pattern of changes, with the exception of the Iguaçu ecoregion. At the inter-ecoregion scale, the changes in mean functional similarity among reservoirs decreased in the first period, -2.3% in 2002/2003, indicating functional differentiation (Fig. 7a). On the contrary, at the 2006/2007 period, the changes in mean functional similarity among reservoirs increased by 0.8%, indicating functional homogenization (Fig. 7a). At the intra-ecoregion scale, the changes in functional

similarity showed contrasting patterns, with Southeastern Mata Atlantica and Upper Paraná ecoregions showing a general tendency towards functional differentiation (Fig. 7b and d), while to the Iguaçu ecoregion the changes in mean functional similarity increased over time (i.e. functional homogenization) (Fig. 7c). To the Southeastern Mata Atlantica ecoregion, the changes in mean functional similarity ranged from -1.6% in 2002/2003 to -0.4% in 2006/2007 (Fig. 7b). For the Iguaçu ecoregion, the changes in mean functional similarity ranged from 0.1% in 2002/2003 to 4.2% in 2006/2007 (Fig. 7c). And to the Upper Paraná ecoregion, the changes in mean functional similarity ranged from -0.4% in 2002/2003 to -1.9% in 2006/2007 (Fig. 7d).
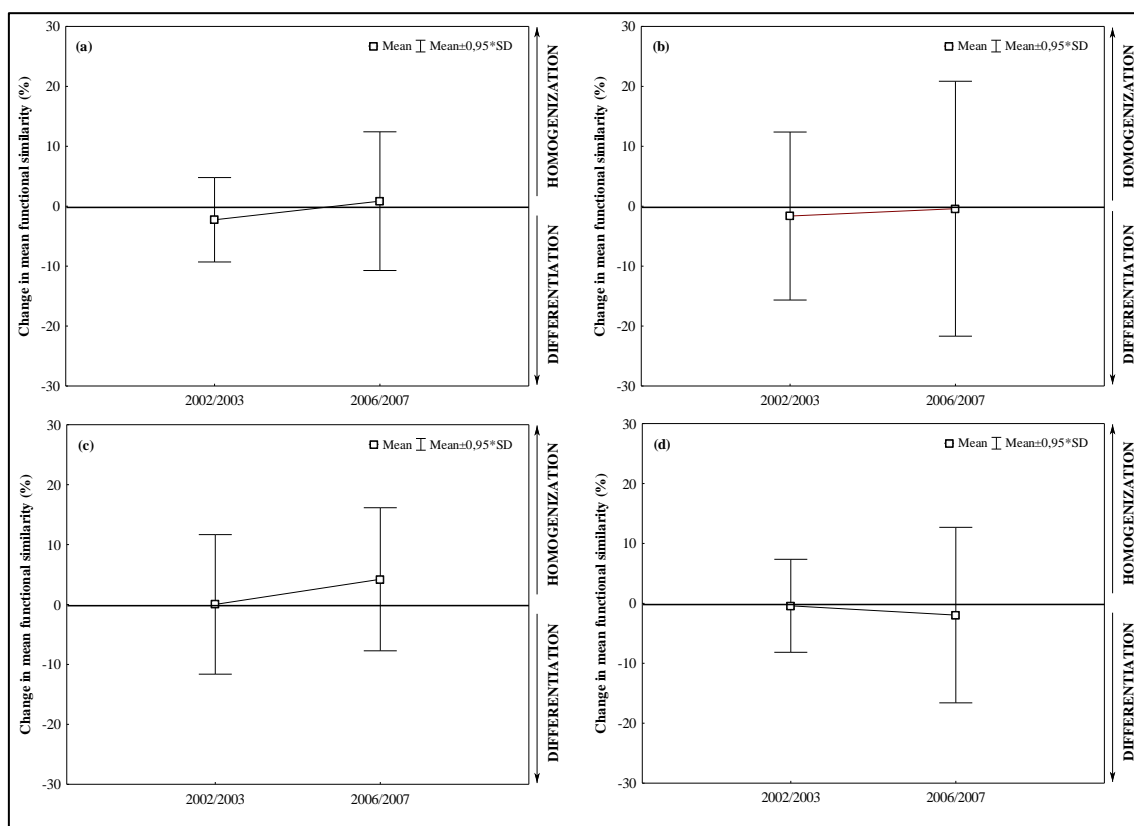
Figure 7 Mean changes in functional similarity among reservoirs at inter-ecoregion and intra-ecoregion scales, for each time period. (a) Inter-ecoregion scale, (b) Southeastern Mata Atlantica, (c) Iguaçu, and (d) Upper Paraná ecoregions. Positive values represented functional homogenization and negative values represented functional differentiation.

At the inter-ecoregion scale, the majority of the changes in functional similarity among pairs of reservoirs from the initial to the 2002/2003 period were negative (79 out of 127 comparisons), indicating functional differentiation (Fig. 8a; Table S3 in Supplementary Material − Appendix 7). By the other hand, changes in functional similarity among pairs of reservoirs from the initial to the 2006/2007 period were positive

(70 out of 127 comparisons), indicating functional homogenization (Fig. 8b; Table S3 in Supplementary Material – Appendix 7). Moreover, the changes in functional similarity among pairs of reservoirs in the current situations were negative (66 out of 127 comparisons between 2002/2003 and 2004/2005 periods) (Fig. 8c), and positive (85 out of 127 comparisons between 2004/2005 and 2006/2007 periods), indicating that in the last period, the addition of species that had similar traits resulted in an increase in functional similarity (i.e. homogenization) (Fig. 8d).

Figure 8 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the inter-ecoregion scale (*n* = 127). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

On the contrary, at the intra-ecoregion scale, the changes in functional similarity were negative for most of the pairwise comparisons, indicating that reservoirs of each ecoregion had become more different about the functional attributes (i.e. functional differentiation), except for the Iguaçu ecoregion, in which the functional composition

among reservoirs had become more similar over time (i.e. functional homogenization) (Table S3 in Supplementary Material – Appendix 7). To the Southeastern Mata Atlantica ecoregion, the majority of the changes in functional similarity among pairs of reservoirs from the initial to the current periods were negative, indicating functional differentiation (Fig. 9a and b; Table S3 in Supplementary Material – Appendix 7). However, the changes in functional similarity among pairs of reservoirs in the current situations were both negative and positive, indicating that in the 2004/2005 period the addition of species with different traits resulted in a decrease in functional similarity (i.e. differentiation) (Fig. 9c), while in the last period, the addition of species that had similar traits led to a increase in functional similarity (i.e. homogenization) (Fig. 9d) (Table S3 in Supplementary Material – Appendix 7).

Figure 9 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the Southeastern Mata Atlantica ecoregion ($n = 6$). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

To the Iguaçu ecoregion, the majority of the changes in functional similarity among pairs of reservoirs from the initial to the current periods were positive (21 out of 36 comparisons between initial and 2002/2003 period, and 23 out of 36 comparisons between initial and 2006/2007 period), indicating functional homogenization (Fig. 10a and b; Table S3 in Supplementary Material − Appendix 7). Moreover, the changes in functional similarity among pairs of reservoirs in the current situations were negative (19 out of 36 comparisons between 2002/2003 and 2004/2005 periods) (Fig. 10c) and positive (21 out of 36 comparisons between 2004/2005 and 2006/2007 periods) (Fig. 10d), indicating that, in the two last periods, the addition of species presenting new traits led to a decrease in functional similarity (i.e. differentiation), while the addition of similar traits resulted in a increase in functional similarity (i.e. homogenization) (Fig. 10c and d) (Table S3 in Supplementary Material – Appendix 7).
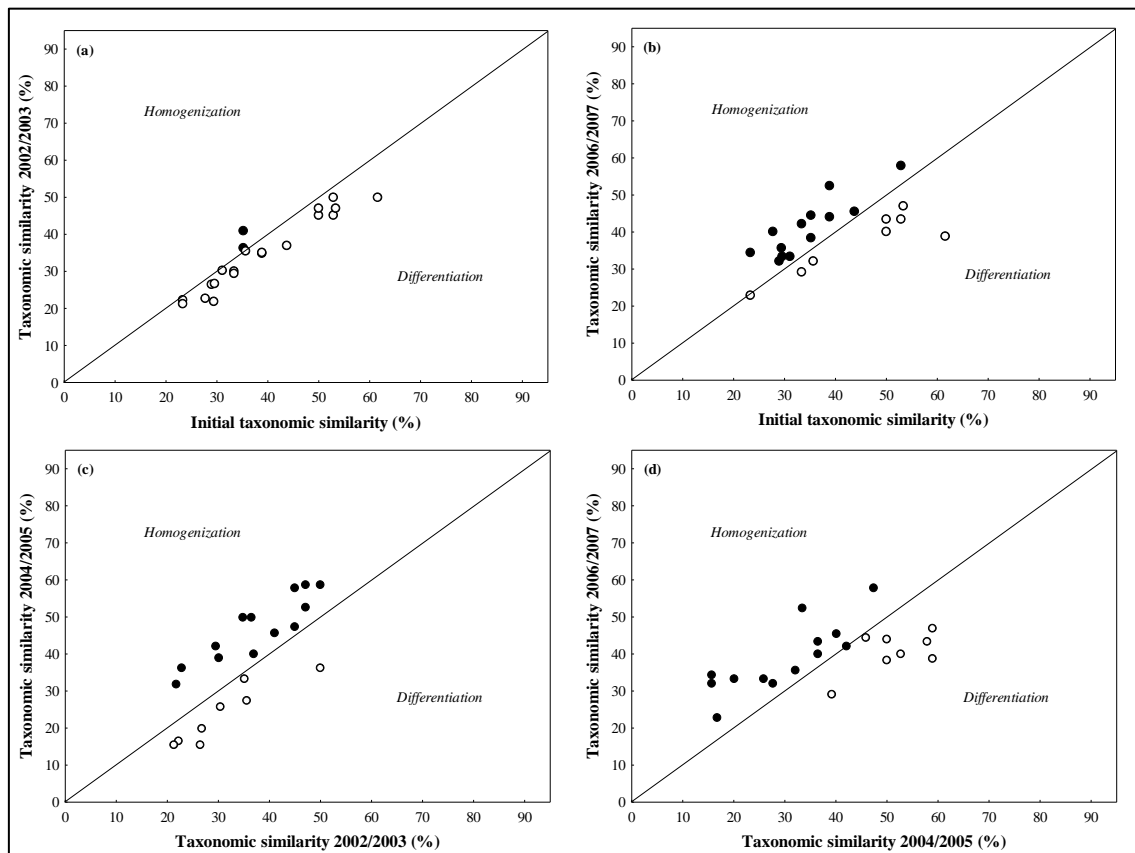

Figure 10 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the Iguaçu ecoregion (*n* = 36). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

To the Upper Paraná ecoregion, the majority of the changes in functional similarity among pairs of reservoirs from the initial to the current periods were negative (11 out of 21 comparisons between initial and 2002/2003 period, and 12 out of 21 comparisons between initial and 2006/2007 period), indicating functional differentiation (Fig. 11a and b; Table S3 in Supplementary Material – Appendix 7). In addition, the changes in functional similarity among pairs of reservoirs in the current situations were negative (11 out of 21 comparisons between 2002/2003 and 2004/2005 periods) (Fig. 11c), and positive (11 out of 21 comparisons between 2004/2005 and 2006/2007 periods), resulting of the addition, in the two last periods, of five species presenting new traits, which led to a decrease in functional similarity (i.e. differentiation) (Fig. 11c and d) (Table S3 in Supplementary Material – Appendix 7).

Figure 11 Current periods versus initial functional similarity for pairwise comparisons among reservoirs at the Upper Paraná ecoregion (*n* = 21). (a) Comparisons between initial similarity and similarity in 2002/2003, (b) comparisons between initial similarity and similarity in 2006/2007, (c) comparisons between similarities in 2002/2003 and 2004/2005, and (d) comparisons between similarities in 2004/2005 and 2006/2007. Filled symbols located above the 1:1 line of equality indicate reservoirs pairs for which functional similarity has increased with time (i.e. functional homogenization), and empty symbols located below the 1:1 line indicate reservoirs pairs for which functional similarity has decreased with time (i.e. functional differentiation).

Changes in the initial, native, native extirpated and non-native assemblages traits composition, at the inter-ecoregion and intra-ecoregion scales, were evident to most of periods analysed (Figs. 12, 13, 14, and 15). At inter-ecoregion scale, at the 2002/2003 period, the major part of the lower-left quadrant of the ordination space was comprised of non-native species, which occupied part of the functional space of native extirpated species. Non-native species exhibit a wide range in the body size and weight, as well as gonad weight and caudal fin aspect. These species also presented predominantly subterminal and terminal mouth position, were benthopelagic and mainly omnivore (Fig. 12a). In the 2004/2005 period, almost the entire lower-right quadrant of the ordination space was comprised of non-native species, which presented large body size, high values to body and gonad weight, as well as to the caudal fin aspect. Whereas the native extirpated species showed a wide range in their functional atributes, presenting predominantly terminal mouth position, demersal and benthopelagic water column position, and belonging to the detritivore and omnivore trophic guild (Fig. 12b). For the 2006/2007 period, non-native species occupied a large part of the functional space of the initial, native and native extirpated assemblages. Non-native species showed large body size, high values to body and gonad weight, as well as to the caudal fin aspect. While native extirpated species showed a wide range in the GSI and presented mainly terminal mouth position (Fig. 12c).
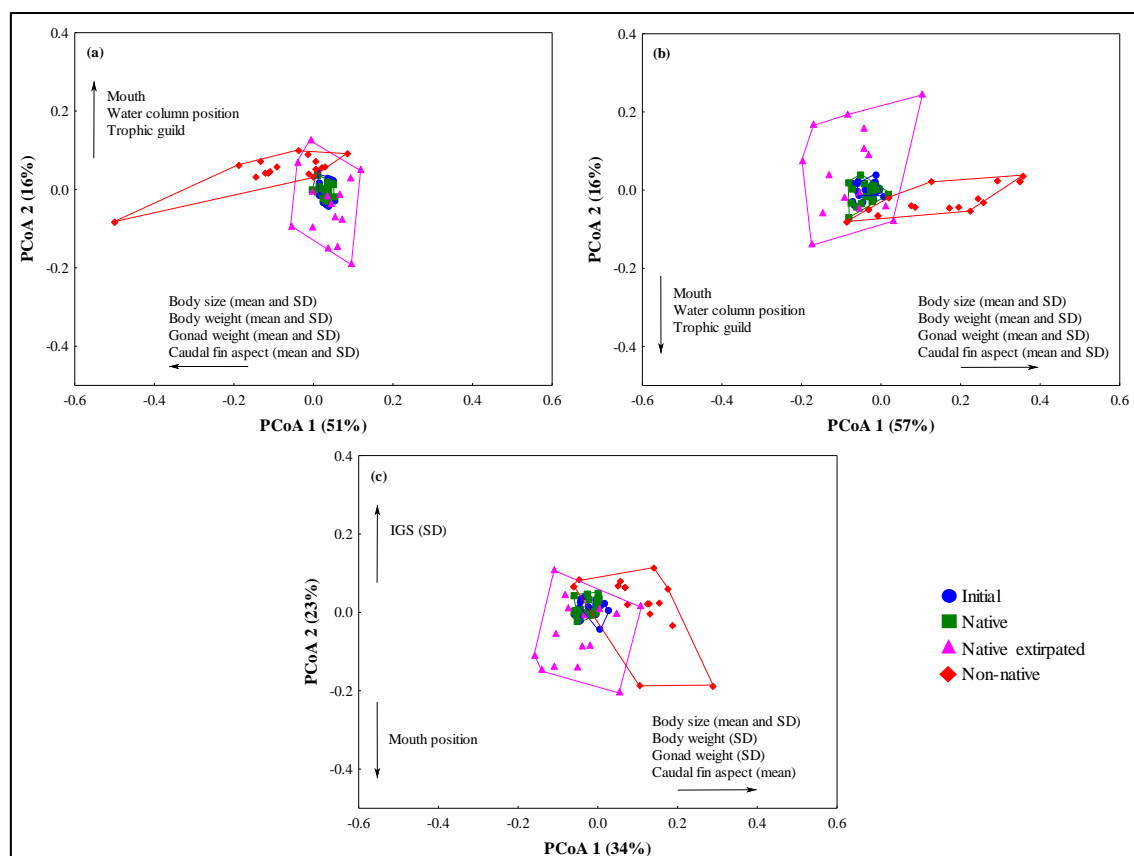
Figure 12 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at inter-ecoregion scale for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

At the intra-ecoregion scales, to the Southeastern Mata Atlantica ecoregion, in the 2002/2003 period, non-native species occuped a "new" part in the functional space, showing generally large body size, high values to body and gonad weight, as well as to the caudal fin aspect and GSI. Whereas the native extirpated species presented predominantly resting and spawned gonad stages, and a small range in the caudal fin aspect and trophic level. Non-native species were mainly omnivore, while native extirpated species were insetivore and omnivore (Fig. 13a). In the 2004/2005 period, non-native species occuped a small part of the functional space of native extirpated species, presenting a wide range in the maturation gonad stage, large body size, high values of body and gonad weight. Whereas the native extirpated species presented terminal and superior mouth position, they were insetivore and omnivore, and showed a small range in the GSI (Fig. 13b). For the 2006/2007 period, non-native species showed generally large body size and high values of body and gonad weight. While native extirpated species presented mainly resting and spawned gonad stages, showing also a wide range in the body size, and a small range in the GSI (Fig. 13c).
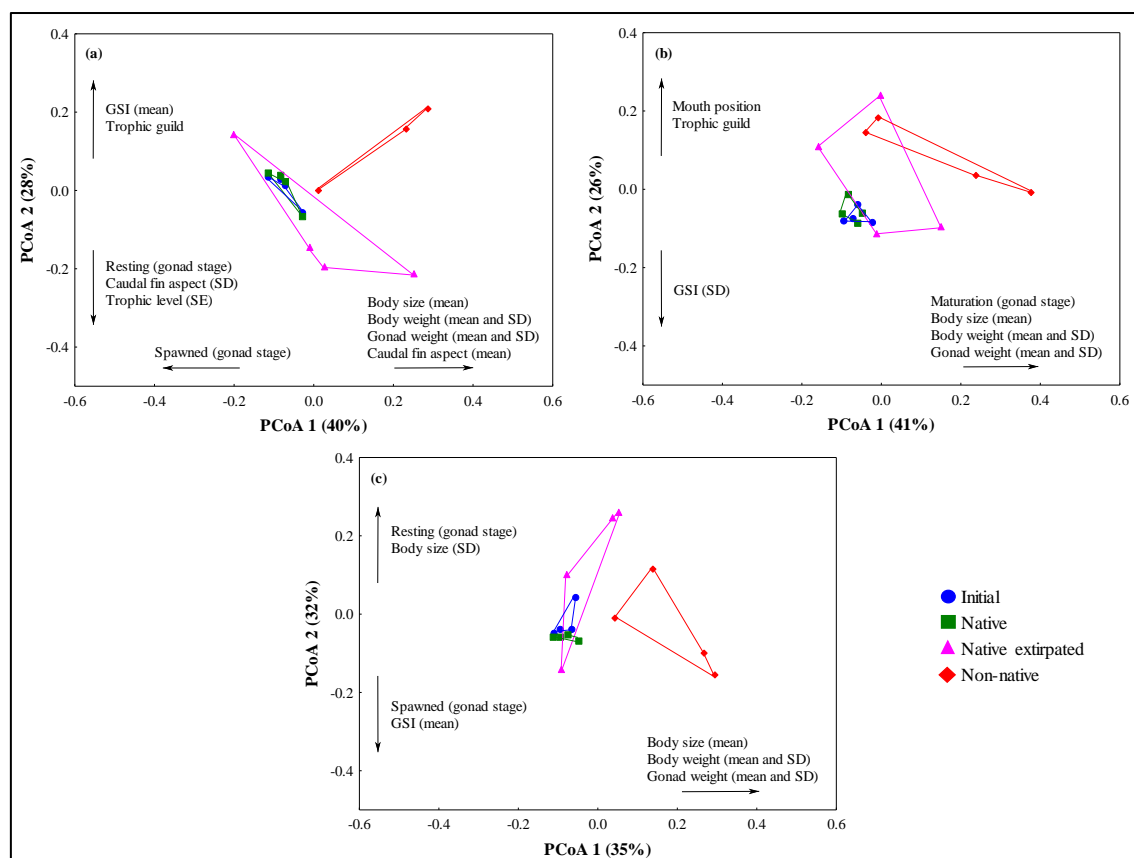
Figure 13 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at the Southeastern Mata Atlantica ecoregion for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

To the Iguaçu ecoregion, in the 2002/2003 period, non-native species occuped a "new" portion in the functional space, presenting predominantly large body size, high values to body and gonad weight, as well as to the caudal fin aspect, and a wide range in the GSI, resting and mature gonad stages. Moreover, these species were mainly benthopelagic. Whereas the native extirpated species presented a small range in the sexual ratio and trophic level (Fig. 14a). In the 2004/2005 period, non-native species occuped a small part of the functional space of initial and native assemblages, presenting large body size, high values to body and gonad weight, as well as to the caudal fin aspect, and being mainly benthopelagic. Whereas the native extirpated species presented a small range in the GSI and trophic level (Fig. 14b). For the 2006/2007 period, non-native species showed a small range in the LWR and high values to trophic level. Moreover, these species presented a wide range in the resting gonad stage, body size, body and gonad weight, and at the caudal fin aspect. While native extirpated species presented a wide range in the trophic level (Fig. 14c).
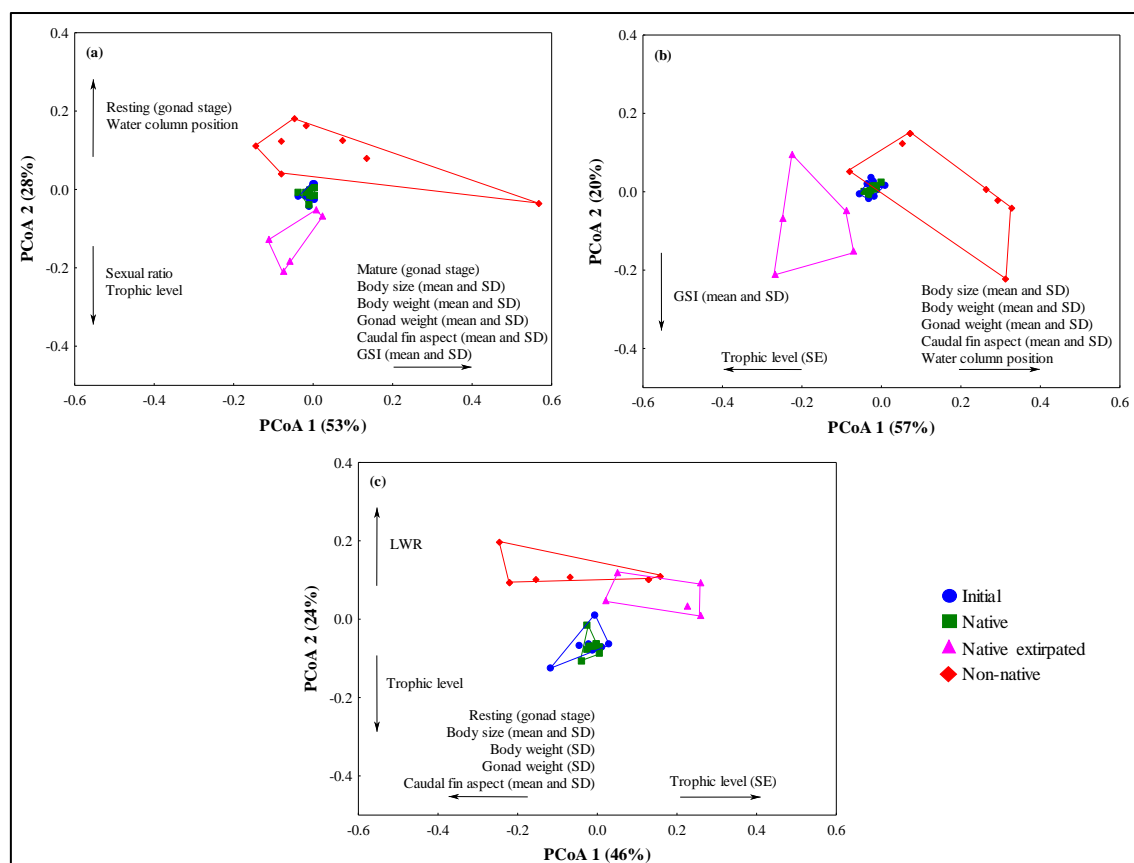
Figure 14 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at the Iguaçu ecoregion for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

To the Upper Paraná ecoregion, in the 2002/2003 period, non-native species occuped a small part of the functional space of native extirpated species, presenting predominantly large body size, high values to body and gonad weight, as well as to the caudal fin aspect. Whereas the native extirpated species presented a wide range in the spawned gonad stage, inferior and terminal mouth position, demersal and benthopelagic water column position, and detritivore trophic guild (Fig. 15a). In the 2004/2005 period, non-native species occuped a part of the functional space of initial and native assemblages, presenting large body size, high values to body and gonad weight. Whereas the native extirpated species presented a small range in the LWR and a wide range in the caudal fin aspect (Fig. 15b). For the 2006/2007 period, non-native species occuped a small part of the initial assemblage functional space, and a large portion of the native assemblage functional space. Non-native species presented a wide range in the maturation gonad stage, possessing large body size, high values to body and gonad weight, subterminal and terminal mouth position, and benthopelagic water column position.

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While native extirpated species presented a small range in the LWR, and a wide range in body size, caudal fin aspect and GSI (Fig. 15c).
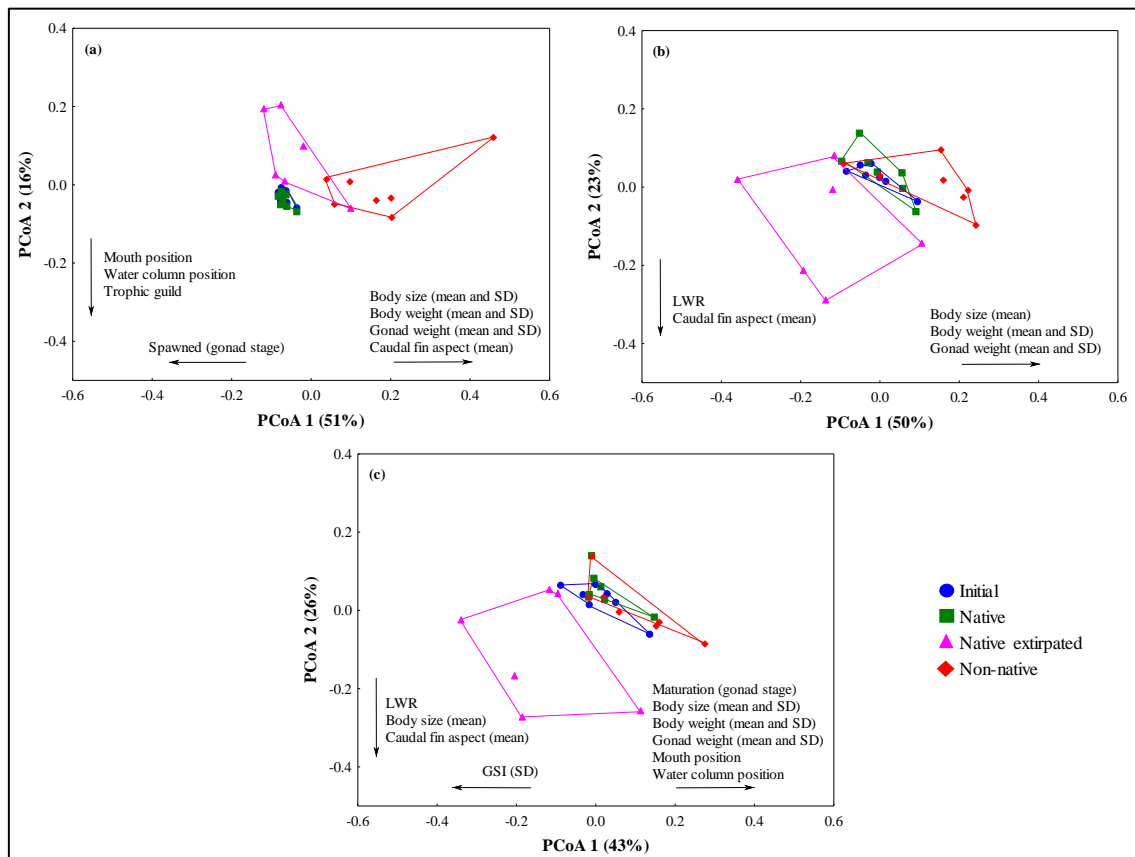
Figure 15 Ordenation of initial, native, native extirpated and non-native assemblages traits composition at the Upper Paraná ecoregion for each time period, along the axes of the first two principal components. (a) 2002/2003, (b) 2003/2004, and (c) 2006/2007.

DISCUSSION

In this study, we quantified the dynamics of changes in the taxonomic and functional composition of freshwater fish fauna in Neotropical reservoirs. We found that changes in fish assemblages were dependent on the spatial and temporal scale. Overall, the homogeneization found in our study, in terms of species composition, was contrasting with the changes in the functional composition of Neotropical freshwater fishes, which influenced the pattern found to the functional homogenization and differentiation. These results were due mainly to the introduction of the same non-native species which possessed similar traits across the reservoirs, as well as to the loss of different native species which exhibited each distinct and similar traits, leading to taxonomic homogenization at the inter-ecoregion scale, while at the same time, it caused the functional differentiation at the first period, and led to the functional homogenizaton in the last period. On the contrary, at the intra-ecoregion scale (i.e. within Southeastern Mata Atlantica and Upper Paraná ecoregions), the taxonomic and functional differentiation may be detected, due to introduction of different non-native species, wich were functionally diverse and replaced native species with similar roles. However, to the Iguaçu ecoregion, the taxonomic differentiation occurred when this ecoregion was functionally homogenizated, due to the extirpation of native species with distinct traits and the introduction of different non-native species, which were functionally redundant.

At the inter-ecoregion scale, we found taxonomic homogenization over time, endorsing the pattern detected to freshwater fish around the world when considering broader spatial scales (Clavero & García-Berthou, 2006; Olden *et al*., 2008; Villéger *et al*., 2011; Marr *et al*., 2013; Liu *et al*., 2017). This pattern was the result of the extirpation of native species, and mainly due to the increasing human-mediated introduction of non-native fish species worldwide (Toussaint *et al*., 2016a). Non-native species coming from other zoogeographic regions, as for example *Cyprinus carpio*, *Oreochromis niloticus* and *Coptodon rendalli*, have spread and established populations in most of the reservoirs in the three study ecoregions. In addition, several extralimital introductions of species as *Astyanax altiparanae*, *Prochilodus lineatus* and *Salminus brasiliensis*, have contributed to the increase in taxonomic similarity at the inter-ecoregion scale. In fact, Liu *et al*. (2017) found that translocated species lead to the greater loss of the compositional distinctiveness of China's freshwater fish faunas than non-native extraregional introductions.

On the contrary, at the intra-ecoregion scale, we found taxonomic differentiation over time. However, this is also a worldwide pattern detected to freshwater fish fauna, especially when finer spatial scales were considered (Taylor, 2004; Marchetti *et al*., 2001; Olden *et al*., 2008; Daga *et al*., 2015). In our study, the differetiaton in terms of species composition was due to the extirpation of native species and the establishement of different non-native species in each reservoir within each ecoregion. For example, *Clarias gariepinus*, *Ictalurus punctatus*, *Hypophthalmichthys nobilis* and *Micropterus salmoides* were originating from other zoogeographic regions, and have successfully established populations in different reservoirs of the major ecoregions here studied, as well as in other ecoregions in the Neotropical region (Vitule *et al*., 2012; Ribeiro *et al*., 2015; Daga *et al*., 2016; Weyl *et al*., 2016). Moreover, Liu *et al*. (2017) demonstrated that in a megadiverse developing country, the compositional similarity of the fish fauna will probably decrease (i.e. taxonomic differentiation) under future scenarios, when considering the contribution of non-native species introduced from other countries. In addition, in our study some extralimital species introductions, as *Leporinus macrocephalus*, *Odontesthes bonariensis* and *Plagioscion squamosissimus* have also established populations in different reservoirs, contributing to the decrease in taxonomic similarity at the intra-ecoregion scale.

According to the changes in functional composition, at the inter-ecoregion scale we found functional differentiation in the first period, mainly due to the introduction and establishment of non-native species exhibiting distinct traits, as well as the extirpation of the native species possessing similar 'roles' in the ecosystem. The fish assemblage in the first period recived non-native species with the following distinct functional traits: large body size and weight, and possessing omnivore and piscivore feeding habits. Generally, non-native species successfully established possess large body length (Vitule *et al*., 2012), as well as piscivore, omnivore and detritivore feeding habits (Moyle & Light, 1996). Moreover, non-native species been piscivores, omnivores and detritivores use resources widely available in aquatic environments, being most likely to became successful invaders when native assemblages were already disrupted and freshwater systems were highly simplified, resulted from human activities (e.g. Moyle & Light, 1996; Pool & Olden, 2012). In addition, our results showed that due to introduction of *H. nobilis* and *O. bonariensis*, the planktivore trophic guild was added, thus contributed to the decrease in the functional similarity at the inter-ecoregion scale, in the first period. By the other hand, in the last period, the addition of the non-native species as *Gymnotus*

sylvius and *P. squamosissimus*, which possess similar traits with the non-native species previously introduced, led to the increase in the functional similarity (i.e. functional homogenization).

The transition from differentiation to homogenization over time has already been reported to species compostion. Firstly, as a consequence of the non-native species introduction and establishment, the fish assemblages become more dissimilar leading to taxonomic differentiation; while in a second moment the extirpation of native species and the non-native species spread throughout the aquatic ecosystem, lead to taxonomic homogenization (Clavero & García-Berthou, 2006; Petesse & Petrere Jr., 2012; Pool & Olden, 2012). Thus, the taxonomic and functional homogenization process are expected to continue in the future (e.g. Liu *et al*., 2017), mainly due to extirpation of native unique species, wich possess specific traits, as well as because of the multiple invasion from non-native species sharing similar traits, through a process termed "over-invasion", in which one invasive species can be able to displace another functionally similar invasive species (e.g. Russel *et al*., 2014; Tekiela & Barney, 2017). In addition, the ecoregions here assessed are already severelly impacted by anthropogenic activities, as habitat modification, selective fish exploitation (i.e. mainly species with unique ecological attributes and/or large body size, which are targed by humans), construction of dams and variation of water level in reservoirs, which *per se* can lead to a reduction on native diversity, while favoring new introductions and the increase in the abundance of some non-native species (e.g. Hoeinghaus *et al*., 2009; Gubiani *et al*., 2010b; Vitule *et al*., 2012; Baumgartner *et al*., 2016).

At the intra-ecoregion scale, the changes in functional composition were different to each ecoregion analysed. The functional homogenization was recorded to the Iguaçu ecoregion, whereas the Southeastern Mata Atlantica and Upper Paraná ecoregions presented functional differentiation. In the Southeastern Mata Atlantica ecoregion, few native species presenting small body size were replaced by several different non-natives, which possessed large body size, mainly presenting omnivore and piscivore feeding habits (for example, *A. altiparanae*, *M. salmoides*, *Pseudoplatystoma corruscans* and *S. brasiliensis*). These non-native species presented distinct traits when compared with native species, which may have determined their successfull establishment in new reservoirs where they had no phylogenetically related species (e.g. Skóra *et al*., 2015).

In Iguaçu ecoregion, the functional homogenization occurred when this basin was taxonomically differentiated. This fact, can be associated to the introduction and

establishment of several non-native species that account for taxonomic differentiation within the ecoregion. Whereas, at the same time, those non-native species were functionally redundant with those native species already occupying this ecoregion, and/or the different non-natives introduced had similar functional traits, leading to the concomitant functional homogenization (*see* Pool & Olden, 2012). For example, the non-native *A. altiparanae* possess similar traits to the native species of *Astyanax*, thus increasing the chances of establishment of this non-native species (e.g. Skóra *et al*., 2015) in most reservoirs of the Iguaçu ecoregion, increasing further the functional similarity of this previously distinct endemic fauna.

In adition, to this ecoregion, native species presenting small body size, detritivore and omnivore feeding habits were replaced by broadly adapted and widespread non-natives, which presented predominantly omnivore feeding habits (*A. altiparanae*, *C. carpio*, *C. gariepinus*, *C. rendalli* and *O. niloticus*). This fact, corroborates with the assertion that the consequences of native species loss can be more severe for functional than taxonomic diversity (Su *et al*., 2015). Moreover, this ecoregion possesses a high demand for sport fishing and aquaculture activities, favoring the increase in the selective introductions of different non-native fishes with similar functional traits shared, aiming to support these activities (Daga *et al*., 2016). This is a concern fact, mainly due to the introduction of the large-bodied piscivorous fishes (Gubiani *et al*., 2010a; Vitule *et al*., 2014), which can have their diet based on small endemic fishes, leading to extirpation of these species (e.g. Moyle & Light, 1996). As was the case with the introduction in 1954, of the Nile perch *Lates niloticus* in Lake Victoria, which led to the extinction of several endemic fish species, as well as the scarcity of other fish species (Cucherousset & Olden, 2011). Additionally, the introduction of the planktivore *O. bonariensis*, in most reservoirs of the Iguaçu ecoregion may have contributed to the pattern of functional homogenization found in this ecoregion. This functional space previously unoccupied by the native assemblage, was favored by the reservoirs construction and has provided suitable availability of resources to the successful establishment and spread of this non-native species (Daga *et al*., 2016; Santa Fé & Gubiani, 2016).

The Upper Paraná ecoregion showed functional differentiation. Already in the early years, the introduction of different non-native species with large body size, mainly being omnivore and piscivore (e.g. *C. gariepinus*, *I. punctatus* and *M. salmoides*), led to the replacement of native species with moderate body size, normally presenting detritivore feeding habits. This fact can have caused severe impact on community

dynamics and ecosystem functions, because for example, native species of detritivores loricariids, that can influence the nutrient cycling processes have been extirpated (e.g. Schindler, 2007; Vitule *et al*., 2017).

In addition, at inter-ecoregion scale in our study, initial and native species showed no major differences in their functional space. Whereas, the functional space for native extirpated and non-native fish species was markedly shared, at inter-ecoregion scale. For example, Petesse & Petrere Jr. (2012) found that the homogenization process in Neotropical reservoirs occurred mainly due to the replacement of native species by functionally similar non-native ones, as well as it was associated to the predation pressure by others non-native predators introduced. On the other hand, at intra-ecoregion scale in our study, generally most of non-native fish species have not shared the functional space with the native extirpated species. Similarly, Olden *et al*. (2006b) found that non-native fish species in the Colorado River basin, possessed distinct functional traits, exhibiting great niche diversity and being able to occupy "new" functional space. Therefore, the changes in the functional composition of fish assemblages, assigned to the introduction of non-native species, can result in severe impacts on the recipient aquatic freshwater ecosystems. Moreover, the increase in non-native large-bodied and great-weight species, normally possessing omnivore and piscivore feeding habitats, can lead to the increase in the competition for resource and further predation pressure on native species, affecting ecosystem functioning (e.g. Olden *et al*., 2006b; Hoeinghaus *et al*. 2009; Weyl *et al*., 2016).

Furthemore, the comprehension of the implications of biodiversity loss on ecosystem dynamics is one of the main conservation concerns (Schindler, 2007). However, studies linking the changes in the functional diversity and ecosystem functions in freshwater habitats are often scarce or underestimated (Gosselin, 2012; Toussaint *et al*., 2016b; Schmera *et al*., 2017). In addition, we can claim that loss of functional diversity of tropical fishes have severe negative effects for ecosystems processes and services (Schindler, 2007; Vitule *et al*., 2017), mainly to Neotropical fishes, which play distinct functions in freshwater habitats (for example, contributing to the nutrient cycles, ecosystem productivity and fishery production), and are under potential threat (e.g. Schindler, 2007; Carolsfeld *et al*., 2003; Hoeinghaus *et al*., 2009; Mormul *et al*., 2012; Vitule *et al*., 2017). Thus, future studies should include ecologically relevant traits, aiming to investigate the relashionship between functional diversity and ecosystem

functions (Holmlund & Hammer, 1999), in order to avoid the simplification and reduction of important ecosystems services provided to human needs (Schindler, 2007).

This is of particular concern, once the non-native species possess different types of impacts (both ecological and economic), which are rarely restricted to a single ecosystem service (Vilá *et al*., 2010). Additionally, our study emphasizes that the introduction of non-native fishes and the extirpation of native species have caused unpredictable changes in the patterns of biotic homogenization process. Overall, our results highlighted the dynamics of the homogenization process by showing that, changes in taxonomic similarity among assemblages cannot be used to predict changes in the functional diversity; i.e. the increase in the taxonomic similarity cannot necessarily be reflected in patterns of changes in functional similarity. In addition, our results were concordant with the general predictions for the biotic homogenization process, showing that transition phases in the dynamics of the taxonomic and functional homogenization can occur at different temporal and spatial scales, which are not captured only in the initial and current comparisons or without considering different spatial grain and extent.

CONSIDERAÇÕES FINAIS

A compreensão da dinâmica do processo de homogeneização biótica é de grande importância, principalmente devido a atual atenção e preocupação dispensada à conservação de peixes de água doce. Neste sentido, é imprescindível elucidar o panorama geral sobre a homogeneização biótica da ictiofauna de água doce, visando identificar áreas prioritárias para estudos futuros os principais mecanismos condutores desse processo. A maioria dos estudos referentes ao processo de homogeneização biótica foram localizados em regiões temperadas, sendo a homogeneização taxonômica o foco primordial dos estudos, os quais foram realizados principalmente em escalas temporais e espaciais amplas, ficando clara a necessidade de maior investigação em escalas mais refinadas, as quais permitem detectar fases de transição desse processo, ou seja, diferenciação e homogeneização biótica. Além disso, os principais mecanismos que impulsionaram o processo de homogeneização em ecossistemas de água doce foram a introdução de peixes não-nativos e a modificação do habitat, sendo a extirpação de espécies nativas pouco avaliada.

Ao avaliar os dados empíricos referentes à comunidade de peixes em reservatórios Neotropicais, foi possível quantificar a dinâmica das mudanças na composição de espécies e atributos funcionais em diferentes escalas espaciais e temporais. Primeiramente, quantificou-se o processo de homogeneização biótica em uma escala mais ampla (interbacias), na qual verificou-se a homogeneização biótica devido, à introdução e estabelecimento das mesmas espécies não-nativas. Enquanto que, em uma escala mais refinada (intrabacias) foi detectada diferenciação biótica, devido ao estabelecimento de diferentes espécies não-nativas em cada reservatório e a extirpação de espécies nativas.

Com base nestes resultados e devido a escassez de estudos quantificando a dinâmica da homogeneização funcional na região Neotropical, quantificou-se a dinâmica das mudanças na composição de espécies e atributos funcionais, relacionados à história de vida, uso de habitat, biologia e ecologia de peixes. Verificou se que em escala inter-ecoregiões, a introdução de espécies não-nativas com traços funcionais similares, e a perda de espécies nativas exibindo traços similares e distintos, levou a homogeneização taxonômica, enquanto foram detectadas fases de transição na composição funcional com diferenciação inicial, seguida por homogeneização no último ano. Quando cada ecoregião foi avaliada separadamente, foi detectada principalmente a diferenciação taxonômica e functional, devido a introdução de diferentes espécies não-nativas, possuindo traços funcionais distintos. No entanto, para a ecoregião do Iguaçu, foi detectada diferenciação taxonômica enquanto houve homogeneização funcional.

FLUXOGRAMA FINAL: Imagem com os principais resultados dos três capítulos apresentados neste trabalho. As linhas contínuas indicam possíveis consequências/implicações dos resultados de cada capítulo; as linhas tracejadas indicam como os resultados de cada capítulo podem estar interagindo e influenciando os resultados encontrados nos demais capítulos. Caixas pontilhadas indicam possíveis ações futuras.

HOMOGENEIZAÇÃO BIÓTICA

Aumento da similaridade taxonômica, funcional ou genética de duas ou mais biotas ao longo do tempo.

- Peixes: primeiro grupo a ser estudado, considerável número de artigos
- Compreender a interação dos mecanismos (introdução, extinção e modificação ambiental)
- Avaliar a dinâmica das escalas temporais e espaciais

Capítulo 1
Organizar e sintetizar informações

Maior número de estudos em regiões temperadas	Maioria dos estudos para homogeneização taxonômica	Avaliação em amplas escalas espaciais e temporais
Falta estudos em regiões megadiversas	Falta estudos para homogeneização funcional	Falta estudos para escalas refinadas

Atualizar revisão

Meta-análise das sub-hipóteses

Capítulo 2
Quantificar a dinâmica do processo em reservatórios

Aquicultura responsável pela introdução de espécies	Interbacias homogeneização taxonômica	Intrabacias diferenciação taxonômica
Ex: Tilápia Carpa		
Outros vetores: Blackbass Peixe-rei Corvina	Introdução das mesmas não-nativas	Introdução de diferentes não-nativas

Capítulo 3
Quantificar os padrões de mudança taxonômica e funcional

Taxonômica		Funcional	
Inter-ecoregião homogeneização taxonômica	Intra-ecoregião diferenciação taxonômica	Inter-ecoregião DF (I) HF (II)	Intra-ecoregião DF HF (*)
Introdução das mesmas não-nativas, com traços similares. Extirpação de nativas com traços similares/diferentes		Introdução de diferentes espécies não-nativas, com traços diferentes. (*) Extirpação de nativas com traços diferentes	

Adicionar dados de coletas recentes

DF: diferenciação funcional
HF: homogeneização funcional

(I) Primeiro período
(II) Segundo período

(*) Iguaçu ecoregião homogeneização funcional

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APÊNDICES

Appendix 1 – Chapter I: Supplementary Material (*Literature search and study selection*)
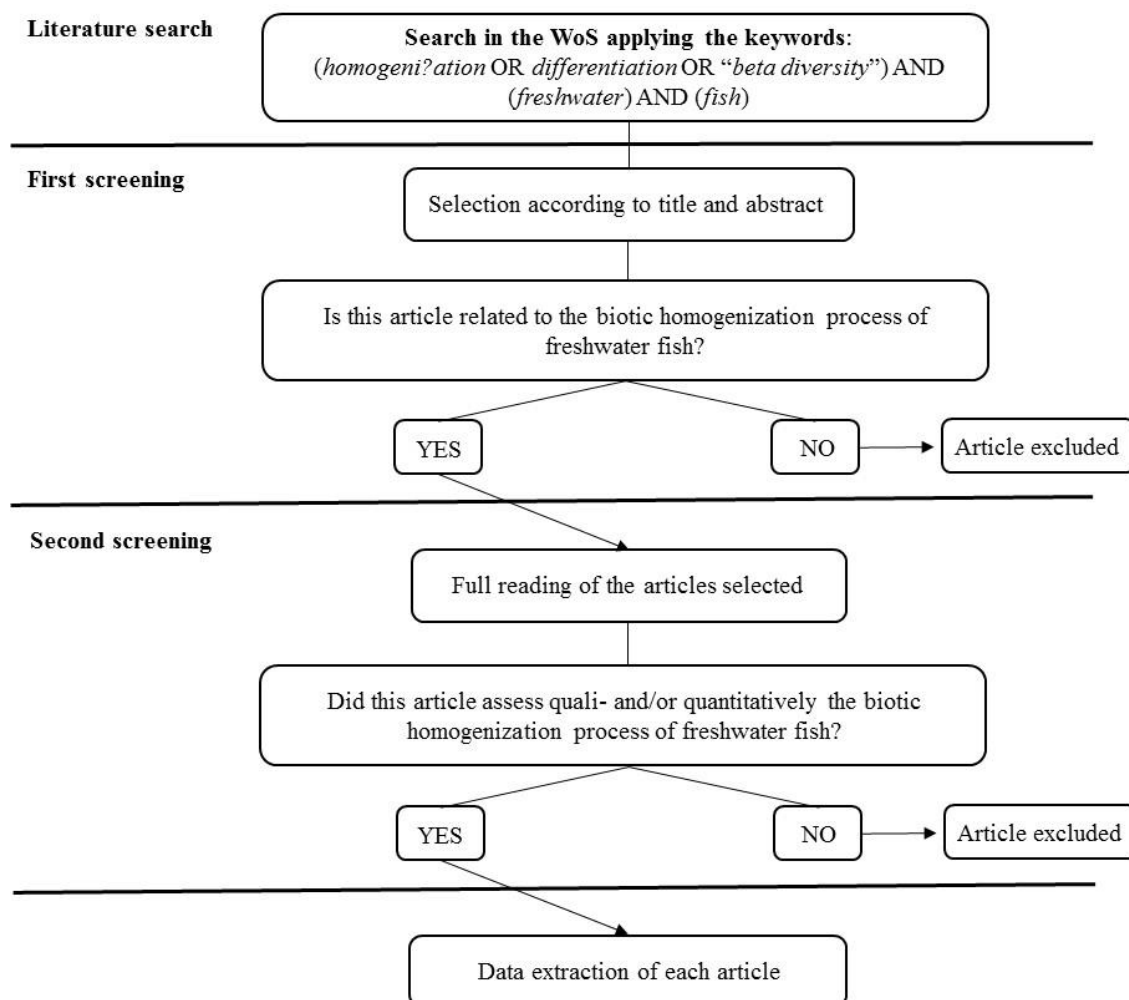
Figure S1. Flowchart representing the steps used in the systematic review and selection criteria for the articles searched in the ISI *Web of Science* (WoS) database. The questions represented the criteria for the selection of the articles in each stage of the screening.
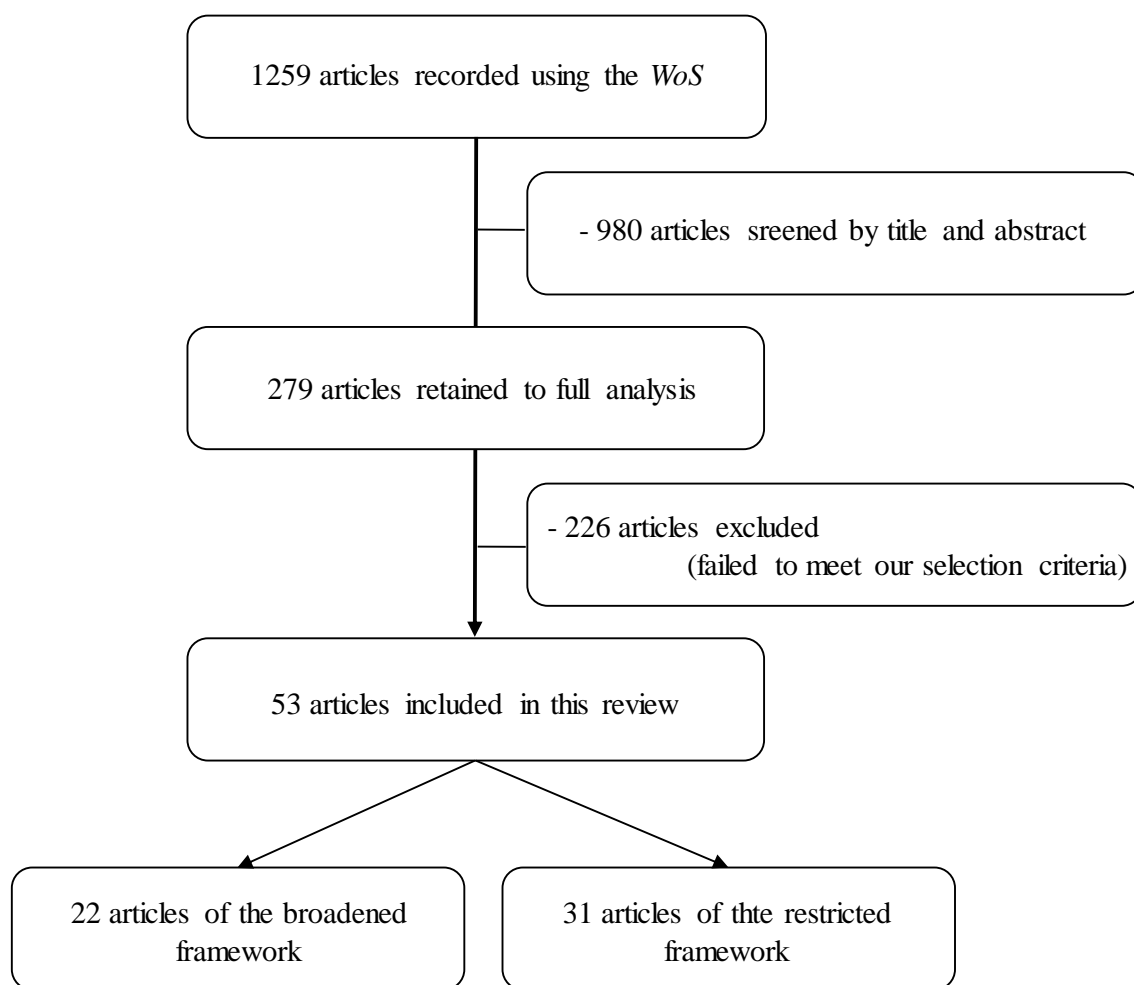
Figure S2. Flowchart representing the steps of the elimination of non-relevant articles according to the first and second screening to this systematic review.

Appendix 2 – Chapter I: Supplementary Material (*Studies included in the analysis*)

Studies included in the analysis, along with their level of support for each sub-hypothesis of the biotic homogenization of freshwater fish hypotheses (supporting, undecided, or questioning).

1. Sub-hypothesis taxonomic homogenization

1.1. Finer temporal scale

1.1.1. Small spatial scale

Supported

Daga, V. D. et al. 2015. Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. – Hydrobiologia 746: 327-347.

Kornis, M. S. et al. 2015. Fish community dynamics following dam removal in a fragmented agricultural stream. – Aquat. Sci. 77: 465-480.

Li, J. et al. 2013. Effects of damming on the biological integrity of fish assemblages in the middle Lancang-Mekong River basin. – Ecol. Indic. 34: 94-102.

Questioned

Daga, V. D. et al. 2015. Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. – Hydrobiologia 746: 327-347.

1.1.2. Moderate spatial scale

Undecided

Daga, V. D. et al. 2015. Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. – Hydrobiologia 746: 327-347.

1.1.3. Large spatial scale

No observations available

1.1.4. Very large spatial scale

Undecided

Clavero, M. and García-Berthou, E. 2006. Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. – Ecol. Appl. 16: 2313-2324.

Questioned

Clavero, M. and García-Berthou, E. 2006. Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. – Ecol. Appl. 16: 2313-2324.

1.2. Large temporal scale

1.2.1. Small spatial scale

Supported

Eberle, M. E. and Channell, R. B. 2006. Homogenization of fish faunas in two categories of streams in a single basin in Kansas and the choice of similarity coefficients. – Trans. Kans. Acad. Sci. 109: 41-46.

Głowacki, L. B. and Penczak, T. 2013. Drivers of fish diversity, homogenization/differentiation and species range expansions at the watershed scale. – Divers. Distrib. 19: 907-918.

Hermoso, V. et al. 2012. Determinants of fine-scale homogenization and differentiation of native freshwater fish faunas in a Mediterranean Basin: implications for conservation. – Divers. Distrib. 18: 236-247.

Hitt, N. P. and Roberts, J. H. 2012. Hierarchical spatial structure of stream fish colonization and extinction. – Oikos 121: 127-137.

Vargas, P. V. et al. 2015. Evaluating taxonomic homogenization of freshwater fish assemblages in Chile. – Rev. Chil. Hist. Nat. 88: 16. doi: 10.1186/s40693-015-0046-2

Undecided

Eberle, M. E. and Channell, R. B. 2006. Homogenization of fish faunas in two categories of streams in a single basin in Kansas and the choice of similarity coefficients. – Trans. Kans. Acad. Sci. 109: 41-46.

Gillette, D. P. et al. 2012. Patterns of change over time in darter (Teleostei: Percidae) assemblages of the Arkansas River basin, northeastern Oklahoma, USA. – Ecography 35: 855-864.

Questioned

Głowacki, L. B. and Penczak, T. 2013. Drivers of fish diversity, homogenization/differentiation and species range expansions at the watershed scale. – Divers. Distrib. 19: 907-918.

Hitt, N. P. and Roberts, J. H. 2012. Hierarchical spatial structure of stream fish colonization and extinction. – Oikos 121: 127-137.

Vargas, P. V. et al. 2015. Evaluating taxonomic homogenization of freshwater fish assemblages in Chile. – Rev. Chil. Hist. Nat. 88: 16. doi: 10.1186/s40693-015-0046-2

1.2.2. Moderate spatial scale

Supported

Cheng, L. et al. 2014. Temporal changes in the taxonomic and functional diversity of fish communities in shallow Chinese lakes: the effects of river–lake connections and aquaculture. – Aquatic Conserv: Mar. Freshw. Ecosyst. 24: 23-34.

Petesse, M. L. and Petrere Jr., M. 2012. Tendency towards homogenization in fish assemblages in the cascade reservoir system of the Tietê river basin, Brazil. – Ecol. Eng. 48: 109-116.

Radomski, P. J. and Goeman, T. J. 1995. The homogenizing of Minnesota lake fish assemblages. – Fisheries 20: 20-23.

Su, G. et al. 2015. Human impacts on functional and taxonomic homogenization of plateau fish assemblages in Yunnan, China. – Glob. Ecol. Conserv. 4: 470-478.

Questioned

Petesse, M. L. and Petrere Jr., M. 2012. Tendency towards homogenization in fish assemblages in the cascade reservoir system of the Tietê river basin, Brazil. – Ecol. Eng. 48: 109-116.

1.2.3. Large spatial scale

Supported

Pool, T. K. and Olden, J. D. 2012. Taxonomic and functional homogenization of an endemic desert fish fauna. – Divers. Distrib. 18: 366-376.

Toussaint, A. et al. 2014. Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide changes in freshwater fish taxonomic dissimilarity. – Glob. Ecol. Biogeogr. 23: 574-584.

Toussaint, A. et al. 2016. Worldwide freshwater fish homogenization is driven by a few widespread non-native species. – Biol. Invasions 18: 1295-1304.

Villéger, S. et al. 2011. Homogenization patterns of the world's freshwater fish faunas. – Proc. Natl. Acad. Sci. USA 108: 18003-18008.

Villéger, S. et al. 2014. Functional homogenization exceeds taxonomic homogenization among European fish assemblages. – Glob. Ecol. Biogeogr. 23: 1450-1460.

Wang, S. et al. 2013. Six decades of changes in vascular hydrophyte and fish species in three plateau lakes in Yunnan, China. – Biodivers. Conserv. 22: 3197-3221.

Questioned

Marchetti, M. P. et al. 2006. Effects of urbanization on California's fish diversity: Differentiation, homogenization and the influence of spatial scale. – Biol. Conserv. 127: 2130-318.

Olden, J. D. et al. 2008. Species invasions and the changing biogeography of Australian freshwater fishes. – Glob. Ecol. Biogeogr. 17: 25-37.

1.2.4. Very large spatial scale

Supported

Clavero, M. and García-Berthou, E. 2006. Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. – Ecol. Appl. 16: 2313-2324.

Hoagstrom, C. W. et al. 2007. Zoogeographic patterns and faunal change of South Dakota fishes. – West. N. Am. Nat. 67: 161-184.

Leprieur, F. et al. 2008. Null model of biotic homogenization: a test with the European freshwater fish fauna. – Divers. Distrib. 14: 291-300.

Marr, S. M. et al. 2010. Freshwater fish introductions in mediterranean-climate regions: are there commonalities in the conservation problem? – Divers. Distrib. 16: 606-619.

Olden, J. D. et al. 2008. Species invasions and the changing biogeography of Australian freshwater fishes. – Glob. Ecol. Biogeogr. 17: 25-37.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. – Science 288: 854-856.

Taylor, E. B. 2004. An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. – Can. J. Fish. Aquat. Sci. 61: 68-79.

Taylor, E. B. 2010.Changes in taxonomy and species distributions and their influence on estimates of faunal homogenization and differentiation in freshwater fishes. – Divers. Distrib. 16: 676-689.

Vitule, J. R. S. et al. 2012. Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. – Divers. Distrib. 18: 111-120.

Watanabe, K. 2012. Faunal structure of Japanese freshwater fishes and its artificial disturbance. – Environ. Biol. Fish. 94: 533-547.

Questioned

Taylor, E. B., 2004. An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. – Can. J. Fish. Aquat. Sci. 61: 68-79.

Taylor, E. B., 2010.Changes in taxonomy and species distributions and their influence on estimates of faunal homogenization and differentiation in freshwater fishes. – Divers. Distrib. 16: 676-689.

2. Sub-hypothesis functional homogenization

2.1. <u>Finer temporal scale</u>

No observations available

2.2. <u>Large temporal scale</u>

2.2.1. Small spatial scale

No observations available

2.2.2. Moderate spatial scale

Supported

Cheng, L. et al. 2014. Temporal changes in the taxonomic and functional diversity of fish communities in shallow Chinese lakes: the effects of river–lake connections and aquaculture. – Aquatic Conserv: Mar. Freshw. Ecosyst. 24: 23-34.

Su, G. et al. 2015. Human impacts on functional and taxonomic homogenization of plateau fish assemblages in Yunnan, China. – Glob. Ecol. Conserv. 4: 470-478.

2.2.3. Large spatial scale

Supported

Pool, T. K. and Olden, J. D. 2012. Taxonomic and functional homogenization of an endemic desert fish fauna. – Divers. Distrib. 18: 366-376.

Villéger, S. et al. 2014. Functional homogenization exceeds taxonomic homogenization among European fish assemblages. – Glob. Ecol. Biogeogr. 23: 1450-1460.

2.2.4. Very large spatial scale

Supported

Marr, S. M. et al. 2013. A global assessment of freshwater fish introductions in mediterranean-climate regions. – Hydrobiologia 719: 317-329.

Vitule, J. R. S. et al. 2012. Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. – Divers. Distrib. 18: 111-120.

Appendix 3 – Chapter I: Supplementary Material (Unweighted tables)

Table S1. Unweighted data from observations supporting, questioning or undecided about the biotic homogenization of freshwater fish communities, both for total and each sub-hypothesis. $\chi 2$ values indicated whether the distribution of the three categories differed from a uniform distribution. $\chi 2$ was calculated only for comparisons with more than five observations. If significant ($P < 0.05$), post hoc binomial tests comparing the proportion of supporting versus questioning observations were performed. Significant results are in bold.

	n	Supported	Undecided	Questioned	χ^2	Binomial test
Total	85	76%	5%	19%	**<0.001**	**<0.001**
Taxonomic	75	74%	5%	21%	**<0.001**	**<0.001**
Functional	10	100%			-	-
Temporal scale						
Finer	9	45%	22%	33%	0.716	**-**
Large	76	80%	3%	17%	**<0.001**	**<0.001**
Spatial scale						
Small	24	50%	8%	42%	**0.030**	0.563
Moderate	9	78%	11%	11%	**0.018**	**0.043**
Large	34	94%		6%	**<0.001**	**<0.001**
Very Large	18	78%	5%	17%	**<0.001**	**0.001**

Table S2. Unweighted data from observations supporting, questioning or undecided about the biotic homogenization process in freshwater fish communities, differentiated according to scenarios, spatial extent and zoogeographic region. χ2 values indicated whether the distribution of the three categories differed from a uniform distribution. χ2 was calculated only for comparisons with more than five observations. If significant ($P < 0.05$), post hoc binomial tests comparing the proportion of supporting versus questioning observations were performed. Significant results are in bold.

	n	Supported	Undecided	Questioned	χ^2	Binomial test
Scenarios						
Invasion-only	24	63%	4%	33%	**0.002**	0.148
Invasion-extinction	61	82%	5%	13%	**<0.001**	**<0.001**
Spatial extent						
River basin	16	88%		12%	**<0.001**	**0.002**
Ecoregion	21	33%	19%	48%	0.276	-
Province	18	78%		22%	**<0.001**	**0.018**
Continent	27	100%			**<0.001**	**<0.001**
Global	3	100%			-	**-**
Zoogeographic region						
Afrotropical	3	100%			-	-
Australian	5	80%		20%	0.075	-
Nearctic	31	81%	6%	13%	**<0.001**	**<0.001**
Neotropical	19	47%	6%	47%	**0.034**	0.818
Oriental	8	100%			-	-
Palearctic	16	81%	6%	13%	**<0.001**	**0.005**
all	3	100%			-	**-**

Appendix 4 – Chapter I: Supplementary Material (Unweighted figures)

Figure S3. Level of support based on unweighted data for the sub-hypothesis type of homogenization. Distinct letters on top of the bars indicate significant differences ($F_{1;85} = 3.08$; $P = 0.08$).

Figure S4. Level of support based on unweighted data for the sub-hypothesis temporal scale. Distinct letters on top of the bars indicate significant differences ($U_{1;85} = 209$; $P < 0.05$).
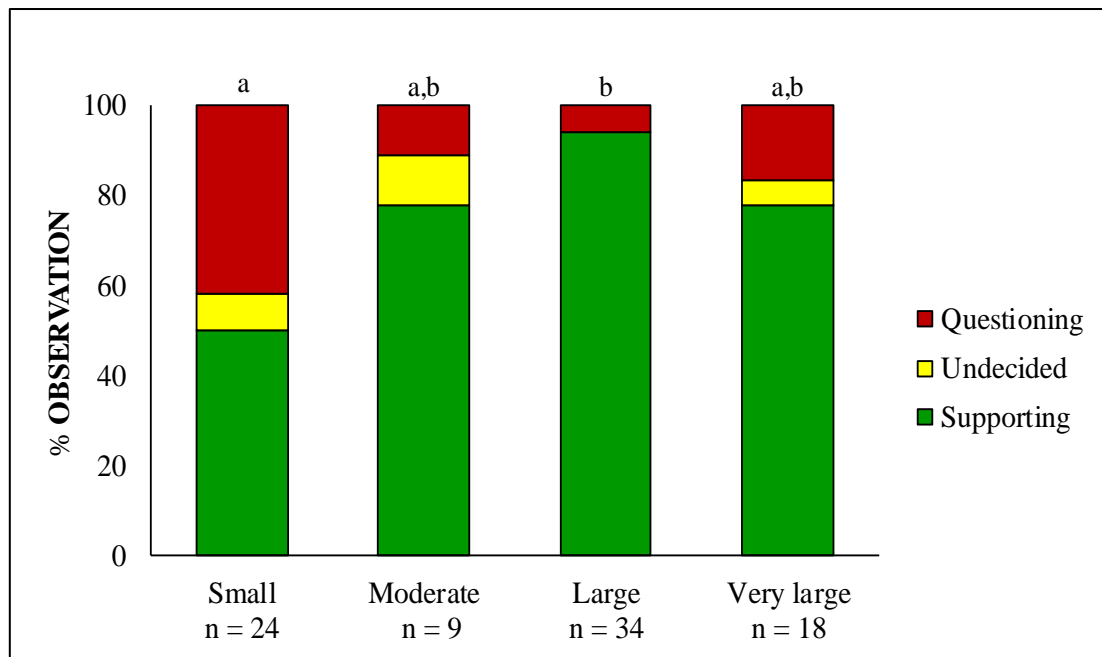
Figure S5. Level of support based on unweighted data for the sub-hypothesis spatial scale. Distinct letters on top of the bars indicate significant differences ($H_{3;85} = 14.80$; $P < 0.05$).

Figure S6. Level of support based on unweighted data for the mechanisms driving homogenization. Distinct letters on top of the bars indicate significant differences ($t_{1;85} = -1.42$; $P = 0.15$).

Figure S7. Level of support based on unweighted data for the spatial extent. Distinct letters on top of the bars indicate significant differences ($H_{4;85} = 32.80$; $P < 0.05$).
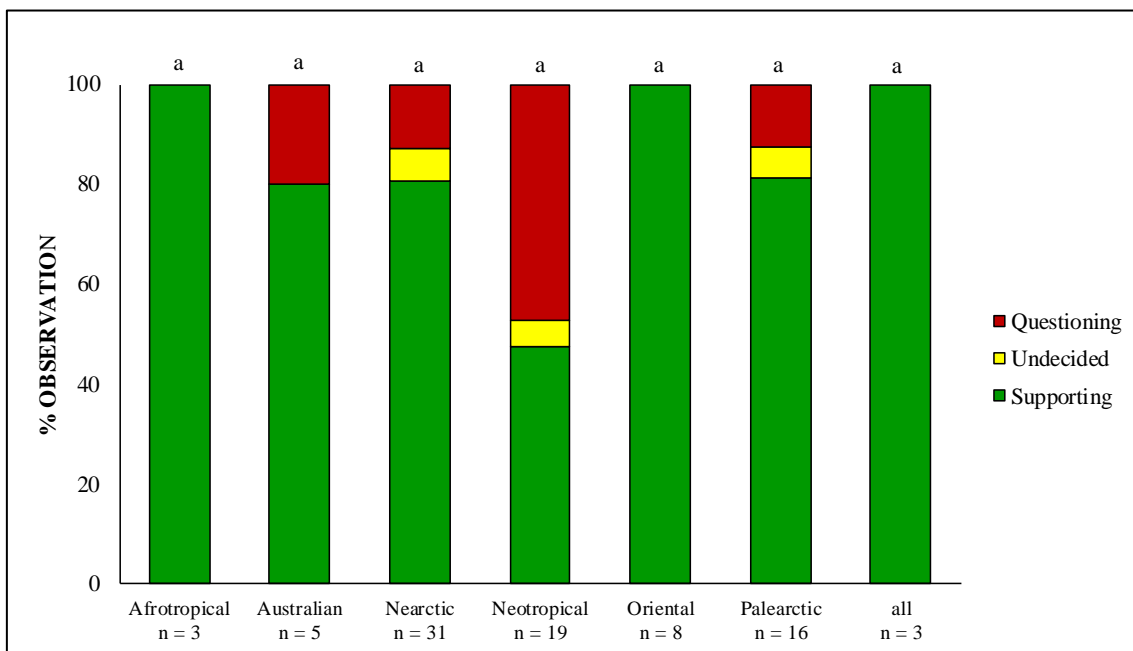
Figure S8. Level of support based on unweighted data for the zoogeopraphic regions. Distinct letters on top of the bars indicate significant differences ($F_{6;85} = 1.66$; $P = 0.14$).

Appendix 5 – Chapter I: Supplementary Material (Weights and percentages of weighted and unweighted observations)

Table S3. Weights and percentages of weighted observations supporting (S), being indecided about (U), or questioning (Q) each sub-hypothesis of the biotic homogenizaton process in freshwater fish hypothesis

		Taxonomic			Funtional			Total		
		S	U	Q	S	U	Q	S	U	Q
Finer temporal scale	Small	3.17 50%		2.82 50%				3.17 50%		2.82 50%
	Moderate		1 100%						1 100%	
	Large									
	Very large		1 50%	1 50%					1 50%	1 50%
Large temporal scale	Small	8.73 50%	3.27 17%	6.00 33%				8.73 50%	3.27 17%	6.00 33%
	Moderate	5.14 83%		0.86 17%	2.00 100%			7.20 88%		0.80 13%
	Large	27.17 96%		0.83 4%	6.00 100%			33.15 97%		0.85 3%
	Very large	12.50 93%		1.50 7%	2.00 100%			14.61 94%		1.39 6%
Total	Small	11.86 50%	3.47 12%	8.67 38%				11.86 50%	3.47 12%	8.67 38%
	Moderate	5.25 72%	0.88 14%	0.88 14%	2.00 100%			7.36 78%	0.82 11%	0.82 11%
	Large	27.17% 96%		0.83% 4%	6.00 100%			33.15 97%		0.85 3%
	Very large	13.79 81%	0.28 6%	1.93 13%	2.00 100%			15.97 83%	0.25 6%	1.77 11%

Table S4. Unweights and percentages of unweighted observations supporting (S), being indecided about (U), or questioning (Q) each sub-hypothesis of the biotic homogenizaton process in freshwater fish hypothesis

		Taxonomic			Funtional			Total		
		S	U	Q	S	U	Q	S	U	Q
Finer temporal scale	Small	4 67%		2 33%				4 67%		2 33%
	Moderate	1 100%						1 100%		
	Large									
	Very large		1 50%	1 50%					1 50%	1 50%
Large temporal scale	Small	8 44%	2 12%	8 44%				8 44%	2 12%	8 44%
	Moderate	5 83%		1 17%	2 100%			7 87%		1 13%
	Large	26 93%		2 7%	6 100%			32 94%		2 6%
	Very large	12 86%		2 14%	2 100%			14 87%		2 13%
Total	Small	12 50%	2 8%	10 42%				12 50%	2 8%	10 42%
	Moderate	5 72%	1 14%	1 14%	2 100%			7 78%	1 11%	1 11%
	Large	26 93%		2 7%	6 100%			32 94%		2 6%
	Very large	12 75%	1 6%	3 19%	2 100%			14 78%	1 5%	3 17%

Appendix 6 – Chapter II: Supplementary material

Table S1 Taxonomic identification of fish species sampled from the pristine sample (=P) and from entire period evaluated (2004 to 2007) for the ecoregions Coastal, Iguaçu and Upper Paraná basins. Status: N (native species for each respective basin), NN (non-native species from the same native biogeographic zone = extralimital in terms of ecoregion or basin) NN (non-native species from other biogeographical zones). The identification of species was based on Oyakawa et al. (2006), Graça & Pavanelli (2007), Baumgartner et al. (2012) and Bifi (2013). (Endemic species of Coastal basin = §; Endemic species of Iguaçu basin = * and Endemic species of Upper Paraná basin = Þ)

Species/Basin	P - COASTAL	COASTAL	P - IGUAÇU	IGUAÇU	P - UPPER PARANÁ	UPPER PARANÁ
Class Actinopterygii – Osteichthyes						
ORDER CYPRINIFORMES						
Family Cyprinidae						
Ctenopharyngodon idella (Valenciennes, 1844)				*NN*		
Cyprinus carpio Linnaeus, 1758		*NN*		*NN*		*NN*
Hypophthalmichthys molitrix (Valenciennes, 1844)				*NN*		
Hypophthalmichthys nobilis (Richardson, 1845)		*NN*		*NN*		
ORDER CHARACIFORMES						
Family Parodontidae						
Apareiodon affinis (Steindachner, 1879)					*N*	*N*
Apareiodon piracicabae Eigenmann, 1907					*N*	*N*
Apareiodon ibitiensis (Amaral-Campos, 1944)					*N*	
Apareiodon vittatus Garavello, 1977 *			*N*	*N*		
Family Curimatidae						
Cyphocharax modestus (Fernández-Yépez, 1948)					*N*	*N*
Cyphocharax santacatarinae (Fernández-Yépez, 1948)			*N*	*N*		
Steindachnerina insculpta (Fernandez & Yepez, 1948) Þ					*N*	*N*
Family Prochilodontidae						
Prochilodus lineatus (Valenciennes, 1836)		*NN*		*NN*	*N*	*N*
Family Anostomidae						

	C1	C2	C3	C4	C5	C6
Leporinus amblyrhynchus Garavello & Britski, 1987 Þ					*N*	*N*
Leporinus friderici (Bloch, 1794)				*NN*		
Leporinus macrocephalus Garavello & Britski, 1988				*NN*	*N*	*N*
Leporinus obtusidens Britski, Birindelli & Garavello, 2012				*NN*	*N*	*N*
Leporinus octofasciatus Steindachner, 1915				*NN*	*N*	*N*
Leporinus piavussu Britski, Birindelli & Garavello, 2012				*NN*		
Schizodon altoparanae Garavello & Britski, 1990 Þ					*N*	*N*
Schizodon nasutus Kner, 1859					*N*	*N*
Family Crenuchidae						
Characidium sp. *			*N*	*N*		
Family Serrasalmidae						
Piaractus mesopotamicus (Holmbreg, 1887)					*N*	*N*
Family Characidae						
Astyanax altiparanae Garutti & Britski, 2000		*NN*		*NN*	*N*	*N*
Astyanax bockmanni Vari & Castro, 2007 Þ					*N*	*N*
Astyanax bifasciatus Garavello & Sampaio, 2010 *			*N*	*N*		
Astyanax dissimilis Garavello & Sampaio, 2010 *			*N*	*N*		
Astyanax fasciatus (Cuvier, 1819)					*N*	*N*
Astyanax gymnodontus Garavello & Sampaio, 2010 *			*N*	*N*		
Astyanax laticeps (Cope, 1894)	*N*	*N*				
Astyanax longirhinus Garavello & Sampaio, 2010 *			*N*	*N*		
Astyanax minor Garavello & Sampaio, 2010 *			*N*	*N*		
Astyanax paranae Eigenmann, 1914					*N*	*N*
Astyanax serratus Garavello & Sampaio, 2010 *			*N*	*N*		
Astyanax sp. 1					*N*	*N*
Astyanax sp. 2					*N*	*N*
Astyanax sp. 3					*N*	*N*
Deuterodon iguape Eigenmann, 1907 §	*N*	*N*				
Deuterodon langei Travassos, 1957 §	*N*	*N*				

Species	1	2	3	4	5	6
Galeocharax knerii (Steindachner, 1870) Þ					N	N
Hyphessobrycon boulengeri (Eigenmann, 1907)	N	N				
Oligosarcus hepsetus (Cuvier, 1829)	N	N				
Oligosarcus longirostris Menezes & Géry, 1983 *			N	N		
Oligosarcus paranensis (Menezes & Géry, 1983) Þ					N	N
Oligosarcus pintoi Campos, 1945 Þ					N	N
Salminus brasiliensis (Cuvier, 1816)		NN		NN	N	N
Brycon hilarii (Valenciennes, 1850)		NN		NN		
Bryconamericus iheringii (Boulenger, 1887)	N	N			N	N
Bryconamericus ikaa Casciotta, Almirón & Azpelicueta, 2004 *			N	N		
Bryconamericus stramineus Eigenmann, 1908					N	
Bryconamericus pyahu Azpelicueta, Casciotta & Almirón, 2004 *			N	N		
Bryconamericus sp. 1					N	N
Bryconamericus sp. 2					N	N
Cyanocharax alburnus (Hensel, 1870)			N	N		
Mimagoniates microlepis (Steindachner, 1877)					N	N
Odontostilbe sp.					N	N
Family Erythrinidae						
Erythrinus erythrinus (Schneider, 1801)					N	
Hoplias intermedius (Günther, 1864)					N	
Hoplias lacerdae Miranda Ribeiro, 1908					N	N
Hoplias malabaricus (Bloch, 1794)	N	N				
Hoplias sp. 1			N	N		
Hoplias sp. A					N	N
Hoplias sp. B					N	N
ORDER SILURIFORMES						
Family Callichthyidae						
Callichthys callichthys (Linnaeus, 1758)					N	N
Corydoras carlae (Nijssen & Isbrücker, 1983) *			N			

	1	2	3	4	5	6
Corydoras ehrhardti Steindachner, 1910	N	N	N	N	N	N
Corydoras paleatus (Jenyns, 1842)	N	N	N	N		
Hoplosternum littorale (Hancock, 1828)			N	N	N	N
Family Loricariidae						
Pareiorhaphis parmula Pereira, 2005 *			N	N		
Isbrueckerichthyes sp.	N	N				
Rineloricaria pentamaculata (Langeani & de Araujo, 1994)					N	
Rineloricaria sp. 1	N	N				
Rineloricaria sp. 2					N	N
Ancistrus sp. 1					N	N
Ancistrus sp. 2			N	N		
Hypostomus albopunctatus (Regan, 1908)			N	N	N	N
Hypostomus ancistroides (Ihering, 1911)	N	N			N	N
Hypostomus aspilogaster (Cope, 1894)	N	N			N	N
Hypostomus commersoni Valenciennes, 1836	N	N	N	N	N	N
Hypostomus derbyi (Haseman, 1911) *			N	N		
Hypostomus interruptus (Miranda-Ribeiro, 1918) §	N	N				
Hypostomus myersi (Gosline, 1947) *			N	N		
Hypostomus nigromaculatus (Schubart, 1964)					N	N
Hypostomus strigaticeps (Regan, 1908) Þ					N	N
Hypostomus paulinus (Ihering, 1905) Þ					N	N
Hypostomus regani (Ihering, 1905)					N	
Hypostomus tapijara Oyakawa, Akama & Zanata, 2005 §	N	N				
Hypostomus sp. 1					N	N
Family Heptapteridae						
Heptapterus sp.			N			
Pimelodella pappenheimi Ahl, 1925 §	N	N				
Rhamdia branneri Haseman, 1911 *			N	N		
Rhamdia quelen (Quoy & Gaimard, 1824)	N	N			N	N

	1	2	3	4	5	6	7	8
Rhamdia voulezi Haseman, 1911 *			*N*	*N*				
Family Ictaluridae								
Ictalurus punctatus (Rafinesque, 1818)				*NN*		*NN*		*NN*
Family Auchenipteridae								
Glanidium melanopterum Miranda Ribeiro, 1918 §	*N*	*N*						
Glanidium ribeiroi Haseman, 1911 *			*N*	*N*				
Tatia neivai (R. von Ihering, 1930) Þ						*N*	*N*	
Tatia jaracatia Pavanelli & Bifi, 2009 *			*N*	*N*				
Family Clariidae								
Clarias gariepinus (Burchell, 1822)						*NN*		*NN*
Family Pimelodidae								
Iheringichthys labrosus (Lutken, 1874)						*N*	*N*	
Pimelodus maculatus Lacépède, 1803						*N*	*N*	
Pimelodus britskii Garavello & Shibatta, 2007 *			*N*	*N*				
Pimelodus ortmanni Haseman, 1911 *			*N*	*N*				
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)				*NN*		*N*	*N*	
Pseudoplatystoma reticulatum Eigenmann & Eigenmann, 1889						*NN*		
Steindachneridion melanodermatum Garavello, 2005 *			*N*	*N*				
ORDER GYMNOTIFORMES								
Family Gymnotidae								
Gymnotus inaequilabiatus (Valenciennes, 1839)	*N*	*N*				*NN*	*N*	*N*
Gymnotus sylvius Albert & Fernandez-Matioli, 1999	*N*	*N*				*NN*		*NN*
Family Sternopygidae								
Eigenmannia trilineata López & Castello, 1966							*N*	
Eigenmannia virescens (Valenciennes, 1842)							*N*	*N*
ORDER ATHERINIFORMES								
Family Atherinopsidae								
Odontesthes bonariensis (Valenciennes, 1835)						*NN*		
ORDER SYNBRANCHIFORMES								

Family Synbranchidae

Synbranchus marmoratus Bloch, 1795					*N*	*N*

ORDER PERCIFORMES

Family Centrarchidade

Micropterus salmoides (Lacépède, 1802)		*NN*				*NN*

Family Cichlidae

Australoheros sp.	*N*	*N*				
Australoheros kaaygua Casciotta, Almirón & Gómez, 2006 *			*N*	*N*		
Australoheros angiru Říčan, Piálek, Almirón & Casciotta, 2011			*N*	*N*		
Cichlasoma paranaense Kullander, 1983					*N*	*N*
Crenicichla iguassuensis Haseman, 1911 *			*N*	*N*		
Crenicichla bristkii Kullander, 1982 Þ					*N*	*N*
Crenicichla haroldoi Luengo & Britski, 1974 Þ					*N*	*N*
Crenicichla niederleinii (Holmberg, 1891)					*N*	*N*
Crenicichla yaha Casciotta, Almirón & Gómez, 2006 *			*N*	*N*		
Geophagus brasiliensis (Quoy & Gaimard, 1824)	*N*	*N*	*N*	*N*	*N*	*N*
Oreochromis niloticus (Linnaeus, 1758)		*NN*		*NN*		*NN*
Tilapia rendalli (Boulenger, 1897)		*NN*		*NN*		*NN*

Family Sciaenidae

*Plagioscion squamosissimu*s (Heckel,1840)						*NN*

Richness of native species	23	23	37	35	64	57
Richness of endemic species	6	6	25	24	12	12
Richness of non-native species from extralimital	-	5	-	13	-	2
Richness of non-native species from other biogeographical zones	-	6	-	8	-	6

Appendix 7 – Chapter III: Supplementary Material
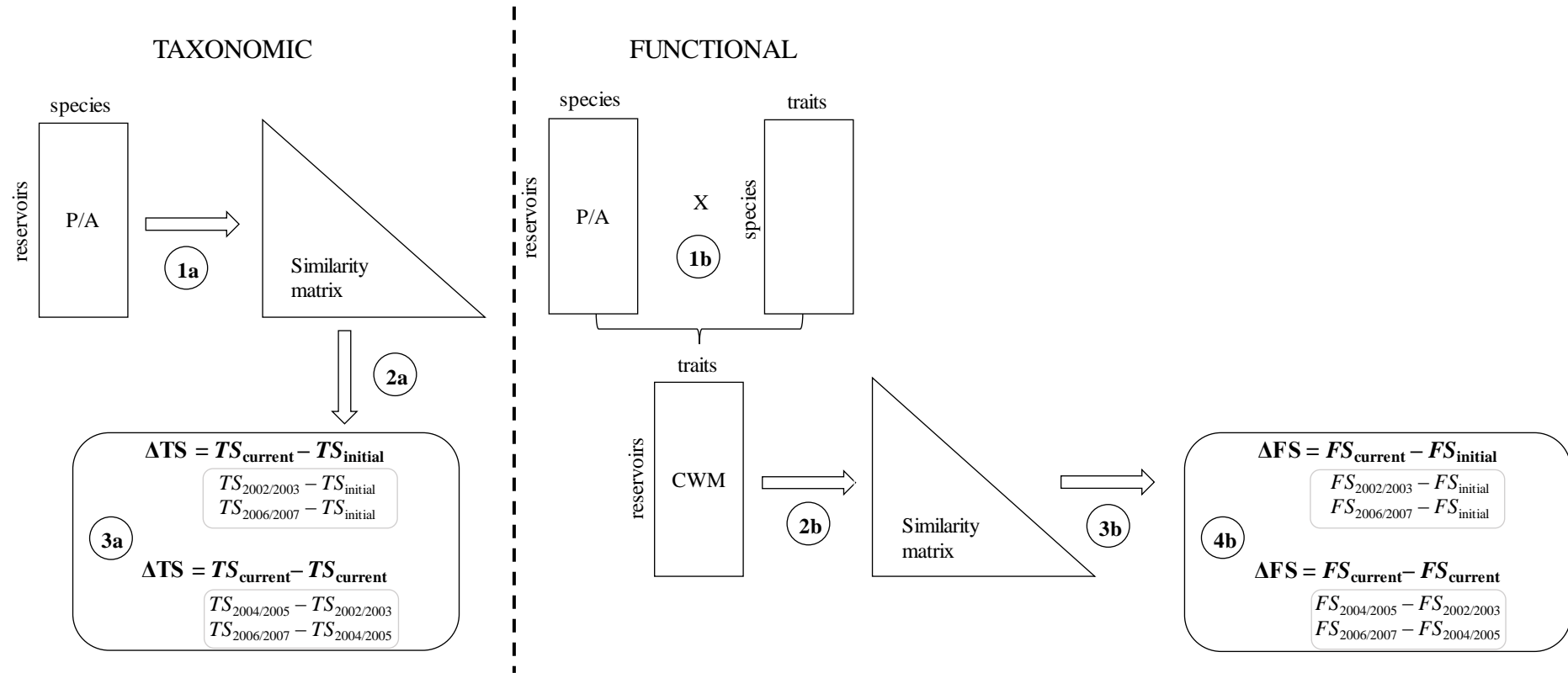
Figure S1 Diagram of the steps of the statistical analyses for inter-ecoregion and intra-ecoregion scales. Taxonomic: 1a - The presence/absence (P/A) data were converted into similarity matrices (using Jaccard's index), for each time period; 2a - Taxonomic similarity matrices (TS) were calculated for the initial assemblage ($TS_{initial}$) and for the assemblages sampled in each current period ($TS_{2002/2003}$, $TS_{2004/2005}$ and $TS_{2006/2007}$); 3a - Changes in pairwise taxonomic similarities were calculated between reservoirs at inter-ecoregion and intra-ecoregion scales for each time period, and measured as current similarity of a pair of reservoirs minus initial similarity of the same pair of reservoirs. Functional: 1b - The CWM reservoir-by-trait matrix was created, by multiplying the reservoir-by-species matrix and species-by-trait matrix for each time period; 2b - The CWM matrices were converted into similarity matrices (using Gower's distance); 3b - Functional similarity matrices (FS) were calculated for the initial assemblage ($FS_{initial}$) and for the assemblages sampled in each current period ($FS_{2002/2003}$, $FS_{2004/2005}$ and $FS_{2006/2007}$); 4a - Changes in pairwise functional similarities were calculated between reservoirs at inter-ecoregion and intra-ecoregion scales for each time period, and measured as current similarity of a pair of reservoirs minus initial similarity of the same pair of reservoirs. Adapted from: Pool & Olden, 2012.

Table S1 Functional traits for 106 fish species

Species	Body length (cm)	Total weight (g)	Gonad weight (g)	GSI	LT/LS relationship (cm)	LWR	Mouth position	Trophic level	Water column position	Trophic guild
Ancistrus sp. 1	8.90	24.10	3.62	15.02	2.40		1		1	1
Ancistrus sp. 2	8.73	22.48	0;95	5.90	2.40	3	1		1	1
Apareiodon affinis	8.60	14.00	2.20	13.80	1.90	3	2	2.2	2	1
Apareiodon piracicabae	9.17	14.72	0.76	5.31	1.90		2	2.3	2	1
Apareiodon vittatus	9.70	18.60	0.87	4.35	2.10	3	1	2.4	2	1
Astyanax altiparanae	7.74	16.20	0.74	3.89	2.14	3	3	2.8	2	3
Astyanax bifasciatus	8.06	14.53	0.54	3.31	2.14	2	3	2.7	2	2
Astyanax bockmanni	7.30	11.95	0.48	3.46	1.98	2	3	2.8	2	3
Astyanax dissimilis	8.08	16.88	0.83	4.55	2.12	3	3	2.7	2	3
Astyanax fasciatus	7.03	8.20	0.42	4.95	1.87	3	3	3,0	2	3
Astyanax gymnodontus	9.72	25.70	1.01	3.64	2.53	3	3	2,0	3	6
Astyanax laticeps	7.67	14.04	0.89	5,09	1.98	3	3	2.8	2	3
Astyanax longirhinus	13.87	82.93	8.03	7.86	3.41	3	3	2.7	2	5
Astyanax minor	7.76	13.45	0.55	3.53	2.15	3	3	2.7	2	3
Astyanax paranae	7.06	8.58	0.53	5.80	1.80	2	3	2.7	2	3
Astyanax serratus	9.48	26.55	1.55	4.92	2.38	3	3	2.7	2	3
Astyanax sp. 1	5.89	5.78	0.51	8.43	1.63	1	3		2	1
Astyanax sp. 2	5.68	5.14	0.47	8.96	1.43	1	3		2	1
Australoheros kaaygua	5.40	9.20	0.88	9.57	1.80		3	3.2	2	1
Australoheros sp.	8.90	35.20	3.45	9.80	2.60		3		2	1
Bryconamericus iheringii	5.69	4.93	0.27	5.86	1.50	3	2	2,0	2	2
Bryconamericus ikaa	5.58	4.56	0.20	4.57	1.46	3	2	2.7	2	3

Species										
Bryconamericus pyahu	5.12	3.43	0.19	5.78	1.23	3	2	2.7	2	3
Bryconamericus stramineus	4.77	2.04	0.14	6.98	1.10	3	3	2.7	2	3
Bryconamericus sp. 1	5.38	4.32	0.28	6.86	1.44	2	3		2	3
Bryconamericus sp. 2	6.30	8.71	0.28	4.39	1.65	2	3		2	3
Characidium sp.	7.07	7.49	0.96	11.24	1.43		2		2	3
Cichlasoma paranaense	6.75	21.80	0.17	1.05	2.41	3	3	3.3	2	6
Clarias gariepinus	63.00	1799.15	21.14	4.62	11.00		2	3.8	2	3
Corydoras carlae	4.70	4.23			1.75		2	3,0	1	1
Corydoras ehrhardti	4.60	4.10	0.36	8.64	1.50	3	2	3.2	1	1
Corydoras paleatus	5.35	6.39	0.47	6.96	1.80	1	2	2.9	1	1
Crenicichla bristkii	8.35	15.21	0.44	2.99	2.38	3	3	3.1	2	6
Crenicichla haroldoi	11.20	36.58	1.85	3.35	2.53	3	3	3.2	2	6
Crenicichla iguassuensis	13.38	69.10	0.84	1.55	2.59	2	3	3.2	2	3
Crenicichla niederleinii	10.61	27.99	0.61	2.87	2.37	3	3	3.2	2	6
Crenicichla yaha	9.25	16.58	0.30	2.01	1.94	1	3	3.2	2	3
Cyanocharax alburnus	5.03	2.62	0.13	4.87	1.20	3	3	3,0	2	6
Cyphocharax modestus	10.96	39.96	2.24	4.76	2.84	3	3		2	1
Cyphocharax santacatarinae	11.59	40.66	1.56	3.62	3.24	1	2		2	1
Cyprinus carpio	53.16	5544.51	882.72	11.72	11.59	3	2	3.1	2	3
Deuterodon iguape	7.67	11.71	0.59	4.68	1.92	2	3	3.1	2	3
Deuterodon langei	7.06	9.22	0.43	4.15	1.87	3	3	3.1	2	3
Eigenmannia trilineata	18.35	17.20	1.62	9.53			3	3.1	2	6
Eigenmannia virescens	20.00	17.70	1.65	9.32			2	3.2	2	6
Geophagus brasiliensis	9,97	56.15	0.77	1.60	2.88	3	3	2.6	2	3
Glanidium ribeiroi	12.02	82.87	2.45	3.60	2.58	3	3	3.4	1	3
Gymnotus inaequilabiatus	27.05	79.98	2.67	2.66			4	3.4	2	6
Gymnotus sylvius	33.48	198.10	7.04	2.76		3	4	3.2	2	6

Species										
Heptapterus sp.	20.50	58.60			4.80		3		1	3
Hoplias intermedius	36.30	1452.75	65.67	4.39	9.23		3	3.6	2	4
Hoplias lacerdae	43.50	1694.00	130.27	7.69	9.00		3	3.7	2	4
Hoplias malabaricus	29.63	757.22	30.52	3.98	6.27	3	3	4.5	2	4
Hoplias sp. 1	32.33	883.72	24.70	2.67	6.70	3	3	4.5	2	4
Hoplias sp. A	26.30	677.25	16.36	3.47	5.57	3	3		2	4
Hoplias sp. B	27.91	598.09	20.57	3.24	5.90	3	3		2	4
Hyphessobrycon boulengeri	4.66	3.40	0.22	6.42	1.44	3	3	2.9	2	3
Hypophthalmichthys nobilis	93.00	29975.00	10481.90	34.97	24.00	3	3	2.8	2	7
Hypostomus ancistroides	15.56	97.87	4.63	4.39	5.17	3	1	2,0	1	1
Hypostomus aspilogaster	21.49	247.57	6.16	2.61	7.25	3	1		1	1
Hypostomus commersoni	22.17	297.28	6.73	1.84	8.39	3	1	2,0	1	1
Hypostomus derbyi	22.58	288.14	8.24	2.27	7.44	3	1		1	1
Hypostomus interruptus	21.47	209.33	9.23	3.71	7.33	3	1		1	1
Hypostomus myersi	15.34	109.94	4.69	4.74	4.50	3	1		1	1
Hypostomus nigromaculatus	9.06	25.01	3.07	12.08	2.75	3	1		1	1
Hypostomus regani	18.80	199.45	3.90	3.00	6.13	3	1		1	1
Hypostomus tapijara	22.24	365.12	17.36	2.87	7.92	3	1		1	1
Hypostomus sp. 1	18.86	165.08	7.24	4.17	6.25	3	1		1	1
Ictalurus punctatus	34.50	1149.25	36.41	1.95	7.75		2	4.2	2	3
Iheringichthys labrosus	16.35	78.24	1.64	2.20	4.29	3	2	2.9	1	3
Leporinus amblyrhynchus	9.15	14.50	0.78	4.67	2.20		2		2	3
Leporinus macrocephalus	41.65	2392.45	9.50	0.41	11.25		3	2,0	2	2
Leporinus obtusidens	36.50	1223.00	7.13	0.58	6.80		3	2,0	2	3
Leporinus octofasciatus	11.73	62.00	4.79	4.58	2.97		3	2,0	2	2
Micropterus salmoides	22.02	445.15	14.39	1.92	4.46	3	4	3.8	2	4
Mimagoniates microlepis	3.67	1.02	0.07	7.93	1.09	3	4	3.2	2	6

Odontesthes bonariensis	18,57	89.58	1.42	1.43	3.43	2	3	2.6	3	7
Odontostilbe sp.	5,92	5.20	0.27	4.92	1.50	3	3		2	3
Oligosarcus hepsetus	16.51	109.14	7.03	4.24	3.72	3	3	4.2	2	4
Oligosarcus longirostris	18.05	134.26	4.51	2.37	4.08	3	3	4.1	2	4
Oligosarcus paranensis	10.04	22.71	0.66	2.49	2.42	3	3	4.1	2	4
Oligosarcus pintoi	9,10	16.20	0.58	4.03	2.15		3	4.2	2	4
Oreochromis niloticus	16.33	195.95	2.37	1.13	4.62	3	3	2,0	2	3
Pimelodella pappenheimi	9,76	15.00	0.49	3.30	2.33	3	3	3.5	1	3
Pimelodus britskii	14.47	82.97	2.53	2.60	4.22	2	3	3.3	1	4
Pimelodus ortmanni	11.47	31.39	0.99	2.46	3.11	2	3	3.3	2	6
Plagioscion squamosissimus	24.50	341.19	3.32	0.80	5.48	3	3	4.4	2	4
Poecilia reticulata	3.10	0.83	0.37	44.58	1.00		4	3.2	2	6
Prochilodus lineatus	39.16	1845.87	59.12	2.20	10.99	3	3	2.2	2	1
Pseudoplatystoma corruscans	72.50	4327.00	17.91	0.41	13.00		2	4.5	1	4
Rhamdia branneri	28.55	478.36	26.03	5.05	6.04	3	3		2	4
Rhamdia quelen	23.22	266.99	11.84	4.02	4.87	3	3	3.9	2	4
Rhamdia voulezi	24.88	348.44	14.28	3.90	5.43	3	3		2	4
Rineloricaria pentamaculata	10.49	10.86	0.85	8.69	1.70		1	2.4	1	1
Rineloricaria sp. 1	11.79	13.28	0.68	5.94	1.87	2	1		1	1
Rineloricaria sp. 2	9.65	5.40	0.24	4.23	1.60		1		1	1
Salminus brasiliensis	44.50	2022.50	31.51	1.39	9.05		3	3.8	2	4
Schizodon altoparanae	19.50	131.27	0.40	0.33	3.73		3	2.5	2	2
Schizodon nasutus	25.57	305.07	29.61	6.35	5.25	3	2	2.8	2	2
Serapinus notomelas	3.23	1.01	0.08	7.73	0.86	3	3	2.2	2	2
Serrapinus sp. 1	4.30	1.28	0.07	5.47	1.10		3		2	2
Steindachneridion melanodermatum	48.88	3774.25	147.26	2.04	10.85	3	3	4.2	1	4
Steindachnerina insculpta	12.25	52.75	0.55	0.95	2.70		3	2.1	2	1

Tatia jaracatia	5.45	5.13	0.51	9.77	1.52	3	3	3.3	1	3
Tatia neivai	5.57	5.08	0.50	8.80	1.52	3	3	3.3	2	3
Coptodon rendalli	13.26	140.60	1.25	0.61	3.77	3	3	2.3	2	3

Body length, Total weight, Gonad weight, IGS and LT/LS relationship = mean values

LWR = (1) negative allometry growth; (2) positive allometry growth; (3) isometric growth

Mouth position = (1) inferior; (2) subterminal; (3) terminal; (4) superior

Water column position = (1) demersal; (2) benthopelagic; (3) pelagic

Trophic guild = (1) detritivore; (2) herbivore; (3) omnivore; (4) piscivore; (5) invertivore; (6) insetivore; (7) planktivore

Table S2 Taxonomic identification of fish species sampled from the initial and current periods evaluated for the ecoregions Southeastern Mata Atlantica (SMA), Iguaçu and Upper Paraná. Status: *N* (native species for each respective ecoregion), *E* (native extirpated species = present in the initial dataset but absent at the dataset of the current periods), *NNT* (non-native species translocated from the same native zoogeographic region = extralimital in terms of ecoregion), *NNZ* (non-native species from other zoogeographic regions = extraregional introductions). The identification of species was based on Oyakawa *et al*. (2006), Graça & Pavanelli (2007), Baumgartner *et al*. (2012) and Bifi (2013). (Endemic species of Southeastern Mata Atlantica ecoregion = §; Endemic species of Iguaçu ecoregion = * and Endemic species of Upper Paraná ecoregion = Þ)

Species/Ecoregion	Initial SMA	SMA	Initial IGUAÇU	IGUAÇU	Initial UPPER PARANÁ	UPPER PARANÁ
Class Actinopterygii – Osteichthyes						
ORDER CYPRINIFORMES						
Family Cyprinidae						
Cyprinus carpio Linnaeus, 1758		*NNZ*		*NNZ*		*NNZ*
Hypophthalmichthys nobilis (Richardson, 1845)				*NNZ*		
ORDER CHARACIFORMES						
Family Parodontidae						
Apareiodon affinis (Steindachner, 1879)					*N*	*N*
Apareiodon piracicabae Eigenmann, 1907					*N*	*N*
Apareiodon vittatus Garavello, 1977 *			*N*	*N*		
Family Curimatidae						
Cyphocharax modestus (Fernández-Yépez, 1948)					*N*	*N*
Cyphocharax santacatarinae (Fernández-Yépez, 1948)			*N*	*N*		
Steindachnerina insculpta (Fernandez & Yepez, 1948) Þ					*N*	*N*
Family Prochilodontidae						
Prochilodus lineatus (Valenciennes, 1836)		*NNT*		*NNT*	*N*	*N*
Family Anostomidae						

Species						
Leporinus amblyrhynchus Garavello & Britski, 1987 Þ					N	E
Leporinus macrocephalus Garavello & Britski, 1988				NNT	N	N
Leporinus obtusidens Britski, Birindelli & Garavello, 2012					N	N
Leporinus octofasciatus Steindachner, 1915					N	N
Schizodon altoparanae Garavello & Britski, 1990 Þ					N	E
Schizodon nasutus Kner, 1859					N	N
Family Crenuchidae						
Characidium sp. *		N	N			
Family Characidae						
Astyanax altiparanae Garutti & Britski, 2000	NNT			NNT	N	N
Astyanax bifasciatus Garavello & Sampaio, 2010 *		N	N			
Astyanax bockmanni Vari & Castro, 2007 Þ					N	N
Astyanax dissimilis Garavello & Sampaio, 2010 *		N	N			
Astyanax fasciatus (Cuvier, 1819)					N	N
Astyanax gymnodontus Garavello & Sampaio, 2010 *		N	N			
Astyanax laticeps (Cope, 1894)	N	N				
Astyanax longirhinus Garavello & Sampaio, 2010 *		N	N			
Astyanax minor Garavello & Sampaio, 2010 *		N	N			
Astyanax paranae Eigenmann, 1914					N	N
Astyanax serratus Garavello & Sampaio, 2010 *		N	N			
Astyanax sp. 1					N	N
Astyanax sp. 2					N	N
Deuterodon iguape Eigenmann, 1907 §	N	N				
Deuterodon langei Travassos, 1957 §	N	N				
Hyphessobrycon boulengeri (Eigenmann, 1907)	N	N				

	Col1	Col2	Col3	Col4	Col5	Col6
Oligosarcus hepsetus (Cuvier, 1829)	N	N				
Oligosarcus longirostris Menezes & Géry, 1983 *			N	N		
Oligosarcus paranensis (Menezes & Géry, 1983) Þ					N	N
Oligosarcus pintoi Campos, 1945 Þ					N	N
Salminus brasiliensis (Cuvier, 1816)		NNT				
Bryconamericus iheringii (Boulenger, 1887)	N	N			N	N
Bryconamericus ikaa Casciotta, Almirón & Azpelicueta, 2004 *			N	N		
Bryconamericus pyahu Azpelicueta, Casciotta & Almirón, 2004 *			N	N		
Bryconamericus stramineus Eigenmann, 1908					N	N
Bryconamericus sp. 1					N	N
Bryconamericus sp. 2					N	N
Cyanocharax alburnus (Hensel, 1870)			N	N		
Mimagoniates microlepis (Steindachner, 1877)	N	N	N	N	N	N
Odontostilbe sp.					N	N
Serapinus notomelas (Eigenmann, 1915)					N	N
Serrapinus sp. 1					N	N
Family Erythrinidae						
Hoplias intermedius (Günther, 1864)					N	E
Hoplias lacerdae Miranda Ribeiro, 1908					N	N
Hoplias malabaricus (Bloch, 1794)	N	N				
Hoplias sp. 1			N	N		
Hoplias sp. A					N	N
Hoplias sp. B					N	N

ORDER SILURIFORMES

Family Callichthyidae

	1	2	3	4	5	6
Corydoras carlae (Nijssen & Isbrücker, 1983) *			N	E		
Corydoras ehrhardti Steindachner, 1910	N	N	N	N	N	N
Corydoras paleatus (Jenyns, 1842)	N	N	N	N		
Family Loricariidae						
Rineloricaria pentamaculata (Langeani & de Araujo, 1994)					N	E
Rineloricaria sp. 1	N	N				
Rineloricaria sp. 2					N	N
Ancistrus sp. 1					N	E
Ancistrus sp. 2			N	N		
Hypostomus ancistroides (Ihering, 1911)	N	N			N	N
Hypostomus aspilogaster (Cope, 1894)	N	N			N	N
Hypostomus commersoni Valenciennes, 1836	N	N	N	N	N	N
Hypostomus derbyi (Haseman, 1911) *			N	N		
Hypostomus interruptus (Miranda-Ribeiro, 1918) §	N	N				
Hypostomus myersi (Gosline, 1947) *			N	N		
Hypostomus nigromaculatus (Schubart, 1964)					N	N
Hypostomus regani (Ihering, 1905)					N	E
Hypostomus tapijara Oyakawa, Akama & Zanata, 2005 §	N	N				
Hypostomus sp. 1					N	N
Family Heptapteridae						
Heptapterus sp.			N	E		
Pimelodella pappenheimi Ahl, 1925 §	N	E				
Rhamdia branneri Haseman, 1911 *			N	N		
Rhamdia quelen (Quoy & Gaimard, 1824)	N	N			N	N
Rhamdia voulezi Haseman, 1911 *			N	N		

Taxon								
Family Ictaluridae								
Ictalurus punctatus (Rafinesque, 1818)								*NNZ*
Family Auchenipteridae								
Glanidium ribeiroi Haseman, 1911 *				*N*	*N*			
Tatia jaracatia Pavanelli & Bifi, 2009 *				*N*	*N*			
Tatia neivai (R. von Ihering, 1930) Þ							*N*	*N*
Family Clariidae								
Clarias gariepinus (Burchell, 1822)						*NNZ*		*NNZ*
Family Pimelodidae								
Iheringichthys labrosus (Lutken, 1874)							*N*	*N*
Pimelodus britskii Garavello & Shibatta, 2007 *				*N*	*N*			
Pimelodus ortmanni Haseman, 1911 *				*N*	*N*			
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)			*NNT*				*N*	*N*
Steindachneridion melanodermatum Garavello, 2005 *				*N*	*N*			
ORDER GYMNOTIFORMES								
Family Gymnotidae								
Gymnotus inaequilabiatus (Valenciennes, 1839)	*N*	*N*				*NNT*	*N*	*N*
Gymnotus sylvius Albert & Fernandez-Matioli, 1999	*N*	*E*						*NNT*
Family Sternopygidae								
Eigenmannia trilineata López & Castello, 1966							*N*	*E*
Eigenmannia virescens (Valenciennes, 1842)							*N*	*N*
ORDER ATHERINIFORMES								
Family Atherinopsidae								
Odontesthes bonariensis (Valenciennes, 1835)						*NNT*		
ORDER CYPRINODONTIFORMES								

Family Poeciliidae

Poecilia reticulata Peters, 1859					*N*	*N*

ORDER PERCIFORMES

Family Centrarchidade

Micropterus salmoides (Lacépède, 1802)		*NNZ*				*NNZ*

Family Cichlidae

Species						
Australoheros sp.	*N*	*N*				
Australoheros kaaygua Casciotta, Almirón & Gómez, 2006 *			*N*	*N*		
Cichlasoma paranaense Kullander, 1983					*N*	*N*
Crenicichla bristkii Kullander, 1982 Þ					*N*	*N*
Crenicichla haroldoi Luengo & Britski, 1974 Þ					*N*	*N*
Crenicichla iguassuensis Haseman, 1911 *			*N*	*N*		
Crenicichla niederleinii (Holmberg, 1891)					*N*	*N*
Crenicichla yaha Casciotta, Almirón & Gómez, 2006 *			*N*	*N*		
Geophagus brasiliensis (Quoy & Gaimard, 1824)	*N*	*N*	*N*	*N*	*N*	*N*
Oreochromis niloticus (Linnaeus, 1758)		*NNZ*		*NNZ*		*NNZ*
Coptodon rendalli (Boulenger, 1897)		*NNZ*		*NNZ*		*NNZ*

Family Sciaenidae

*Plagioscion squamosissimu*s (Heckel,1840)						*NNT*

Total of native species	22	20	34	32	54	47
Total of endemic species	5	4	24	23	8	6
Total of extirpated species		2		2		7
Total of non-native species translocated	-	4	-	5	-	2
Total of non-native species from other biogeographical zones	-	4	-	5	-	6

Table S3 Summary of taxonomic and functional similarities for historical and current periods. Temporal changes are indicated by the current value minus the initial one. Values are mean ± standard deviation and ranges in parentheses.

		Taxonomic	Functional
	Initial similarity	0.05 ± 0.04 (0.01; 0.18)	0.68 ± 0.07 (0.45; 0.83)
	2002/2003 similarity	0.09 ± 0.05 (0.01; 0.36)	0.66 ± 0.09 (0.39; 0.80)
	Change (2002/2003-Initial)	-0.03 ± 0.04 (-0.04; 0.25)	-0.02 ± 0.07 (-0.20; 0.16)
Inter ecoregion	2006/2007 similarity	0.10 ± 0.05 (0.02; 0.27)	0.69 ± 0.09 (0.41; 0.84)
	Change (2006/2007-Initial)	0.05 ± 0.04 (-0.05; 0.22)	-0.01 ± 0.12 (-0.39; 0.26)
	2004/2005 similarity	0.11 ± 0.06 (0.03; 0.31)	0.64 ± 0.09 (0.42; 0.88)
	Change (2004/2005-2002/2003)	0.02 ± 0.04 (-0.10; 0.15)	-0.02 ± 0.10 (-0.31; 0.21)
	Change (2006/2007-2004/2005)	-0.01 ± 0.03 (-0.08; 0.09)	-0.05 ± 0.12 (-0.31; 0.34)
	Initial similarity	0.49 ± 0.17 (0.38; 0.81)	0.46 ± 0.20 (0.21; 0.78)
	2002/2003 similarity	0.43 ± 0.11 (0.28; 0.56)	0.45 ± 0.13 (0.20; 0.57)
	Change (2002/2003-Initial)	-0.06 ± 0.11 (-0.26; 0.07)	-0.02 ± 0.15 (-0.25; 0.18)
Southeastern Mata Atlantica ecoregion	2006/2007 similarity	0.48 ± 0.13 (0.28; 0.69)	0.45 ± 0.11 (0.30; 0.62)
	Change (2006/2007-Initial)	-0.01 ± 0.11 (-0.13; 0.11)	-0.01 ± 0.22 (-0.29; 0.28)
	2004/2005 similarity	0.46 ± 0.10 (0.33; 0.56)	0.44 ± 0.15 (0.21; 0.60)
	Change (2004/2005-2002/2003)	0.03 ± 0.10 (-0.06; 0.21)	-0.01 ± 0.11 (-0.19; 0.13)
	Change (2006/2007-2004/2005)	0.03 ± 0.10 (-0.05; 0.18)	-0.01 ± 0.11 (-0.11; 0.16)
	Initial similarity	0.61 ± 0.17 (0.27; 0.84)	0.62 ± 0.13 (0.38; 0.83)
Iguaçu ecoregion	2002/2003 similarity	0.54 ± 0.15 (0.23; 0.78)	0.62 ± 0.13 (0.33; 0.86)
	Change (2002/2003-Initial)	-0.07 ± 0.04 (-0.16; -0.01)	0.001 ± 0.12 (-0.27; 0.27)
	2006/2007 similarity	0.59 ± 0.16 (0.30; 0.90)	0.67 ± 0.10 (0.49; 0.84)

	Change (2006/2007-Initial)	-0.02 ± 0.09 (-0.26; 0.15)	-0.04 ± 0.12 (-0.20; 0.25)
	2004/2005 similarity	0.59 ± 0.17 (0.27; 0.92)	0.62 ± 0.14 (0.24; 0.91)
	Change (2004/2005-2002/2003)	0.05 ± 0.06 (-0.14; 0.18)	-0.006 ± 0.14 (-0.22; 0.28)
	Change (2006/2007-2004/2005)	-0.001 ± 0.07 (-0.14; 0.14)	0.05 ± 0.14 (-0.26; 0.34)
Upper Paraná ecoregion	Initial similarity	0.39 ± 0.11 (0.23; 0.62)	0.59 ± 0.12 (0.30; 0.82)
	2002/2003 similarity	0.35 ± 0.10 (0.21; 0.50)	0.58 ± 0.10 (0.40; 0.73)
	Change (2002/2003-Initial)	-0.04 ± 0.04 (-0.12; 0.06)	-0.01 ± 0.08 (-0.18; 0.12)
	2006/2007 similarity	0.40 ± 0.08 (0.23; 0.58)	0.57± 0.10 (0.37; 0.75)
	Change (2006/2007-Initial)	0.01 ± 0.09 (-0.23; 0.13)	-0.02 ± 0.15 (-0.32; 0.29)
	2004/2005 similarity	0.38 ± 0.14 (0.16; 0.59)	0.58 ± 0.10 (0.38; 0.75)
	Change (2004/2005-2002/2003)	0.03 ± 0.09 (-0.14; 0.15)	-0.002 ± 0.12 (-0.16; 0.23)
	Change (2006/2007-2004/2005)	0.01 ± 0.11 (-0.20; 0.19)	-0.01 ± 0.14 (-0.30; 0.29)

Appendix 8 – Chapter III: Supplementary Material (*Scripts of the analyzes***)**

Quantification of the taxonomic homogenization process

1. Inter-ecoregion

library (vegan)

read.table("AlNTP.txt", header=TRUE)->AlNTP # initial presence/absence data

AlNTP

1-(vegdist(AlNTP, method="jaccard"))->AlP.d # initial similatity matrix

AlP.d

read.table("AlNT23.txt", header=TRUE)->AlNT23 # 2002/2003 presence/absence data

AlNT23

1-(vegdist(AlNT23, method="jaccard"))->Al23.d # 2002/2003 similatity matrix

Al23.d

read.table("AlNT45.txt", header=TRUE)->AlNT45 # 2004/2005 presence/absence data

AlNT45

1-(vegdist(AlNT45, method="jaccard"))->Al45.d # 2004/2005 similatity matrix

Al45.d

read.table("AlNT67.txt", header=TRUE)->AlNT67 # 2006/2007 presence/absence data

AlNT67

1-(vegdist(AlNT67, method="jaccard"))->Al67.d # 2006/2007 similatity matrix

Al67.d

Changes in pairwise taxonomic similarities

Al23.d-AlP.d->deltaAl23 # 2002/2003 similatity – initial similatity

deltaAl23

Al67.d-AlP.d->deltaAl67 # 2006/2007 similatity – initial similatity

deltaAl67

Al45.d-Al23.d->deltaAlT1 # 2004/2005 similatity – 2002/2003 similatity

deltaAlT1

Al67.d-Al45.d-> deltaAlT2 # 2006/2007 similatity – 2004/2005 similatity

deltaAlT2

1.1. Intra-ecoregion

1.1.1. <u>Southeastern Mata Atlantica ecoregion</u>

library (vegan)

read.table("CoastalNEW.txt", header=TRUE)->CoN # presence/absence data

CoN

1-(vegdist(CoN[1:4,], method="jaccard"))->simc23N # initial similatity matrix

simc23N

1-(vegdist(CoN[5:8,], method="jaccard"))->simc23T # 2002/2003 similatity matrix

simc23T

1-(vegdist(CoN[13:16,], method="jaccard"))->simc45T # 2004/2005 similatity matrix

simc45T

1-(vegdist(CoN[21:24,], method="jaccard"))->simc67T # 2006/2007 similatity matrix

simc67T

Changes in pairwise taxonomic similarities

simc23T-simc23N->delta23 # 2002/2003 similatity – initial similatity

delta23

simc67T-simc23N->delta67 # 2006/2007 similatity – initial similatity

delta67

simc45T-simc23T->deltaT1 # 2004/2005 similatity – 2002/2003 similatity

deltaT1

simc67T-simc45T->deltaT2 # 2006/2007 similatity – 2004/2005 similatity

deltaT2

1.1.2. <u>Iguaçu ecoregion</u>

library (vegan)

read.table("IguaNEW.txt", header=TRUE)->IgN # presence/absence data

IgN

1-(vegdist(IgN[1:9,], method="jaccard"))->simi23N # initial similarity matrix

simi23N

1-(vegdist(IgN[10:18,], method="jaccard"))->simi23T # 2002/2003 similatity matrix

simi23T

1-(vegdist(IgN[28:36,], method="jaccard"))->simi45T # 2004/2005 similatity matrix

simi45T

```
1-(vegdist(IgN[46:54,], method="jaccard"))->simi67T # 2006/2007 similatity matrix
simi67T


# Changes in pairwise taxonomic similarities
simi23T-simi23N->deltai23 # 2002/2003 similatity – initial similatity
deltai23
simi67T-simi23N->deltai67 # 2006/2007 similatity – initial similatity
deltai67
simi45T-simi23T->deltaiT1 # 2004/2005 similatity – 2002/2003 similatity
deltaiT1
simi67T-simi45T->deltaiT2 # 2006/2007 similatity – 2004/2005 similatity
deltaiT2
```

1.1.3.   <u>Upper Paraná ecoregion</u>

```
library (vegan)
read.table("UpperNEW.txt", header=TRUE)->UpN # presence/absence data
UpN
1-(vegdist(UpN[1:7,], method="jaccard"))->simu23N # initial similatity matrix
simu23N
1-(vegdist(UpN[8:14,], method="jaccard"))->simu23T # 2002/2003 similatity matrix
simu23T
1-(vegdist(UpN[22:28,], method="jaccard"))->simu45T # 2004/2005 similatity matrix
simu45T
1-(vegdist(UpN[36:42,], method="jaccard"))->simu67T # 2006/2007 similatity matrix
simu67T


# Changes in pairwise taxonomic similarities
simu23T-simu23N->delta23 # 2002/2003 similatity – initial similatity
delta23
simu67T-simu23N->delta67 # 2006/2007 similatity – initial similatity
delta67
simu45T-simu23T->deltaT1 # 2004/2005 similatity – 2002/2003 similatity
deltaT1
simu67T-simu45T->deltaT2 # 2006/2007 similatity – 2004/2005 similatity
deltaT2
```

Quantification of the functional homogenization process

2. Inter-ecoregion

library (FD)

library (vegan)

read.table("AlNFP.txt", header=TRUE)->AlNFP # inicial species-by-traits data

AlNFP

read.table("AlNTP.txt", header=TRUE)->AlNTP # inicial reservoir-by-species data

AlNTP

functcomp(AlNFP,as.matrix(AlNTP))->AlP # inicial CWM matrix

AlP

1-(vegdist(AlP, method="gower"))->AlP.d # initial similatity matrix

AlP.d

read.table("AlNF23.txt", header=TRUE)->AlNF23 # 2002/2003 species-by-traits data

AlNF23

read.table("AlNT23.txt", header=TRUE)->AlNT23 # 2002/2003 reservoir-by-species data

AlNT23

functcomp(AlNF23,as.matrix(AlNT23))->Al23 # 2002/2003 CWM matrix

Al23

1-(vegdist(Al23, method="gower"))->Al23.d # 2002/2003 similatity matrix

Al23.d

read.table("AlNF45.txt", header=TRUE)->AlNF45 # 2004/2005 species-by-traits data

AlNF45

read.table("AlNT45.txt", header=TRUE)->AlNT45 # 2004/2005 reservoir-by-species data

AlNT45

functcomp(AlNF45,as.matrix(AlNT45))->Al45 # 2004/2005CWM matrix

Al45

1-(vegdist(Al45, method="gower"))->Al45.d # 2004/2005 similatity matrix

Al45.d

read.table("AlNF67.txt", header=TRUE)->AlNF67 # 2006/2007 species-by-traits data

AlNF67

read.table("AlNT67.txt", header=TRUE)->AlNT67 # 2006/2007 reservoir-by-species data

AlNT67

functcomp(AlNF67,as.matrix(AlNT67))->Al67 # 2006/2007CWM matrix

Al67

1-(vegdist(Al67, method="gower"))->Al67.d # 2006/2007 similatity matrix

Al67.d

Changes in pairwise functional similarities

Al23.d-AlP.d->deltaAl23 # 2002/2003 similatity – initial similatity

deltaAl23

Al67.d-AlP.d->deltaAl67 # 2006/2007 similatity – initial similatity

deltaAl67

Al45.d-Al23.d->deltaAlT1 # 2004/2005 similatity – 2002/2003 similatity

deltaAlT1

Al67.d-Al45.d-> deltaAlT2 # 2006/2007 similatity – 2004/2005 similatity

deltaAlT2

2.1. Intra-ecoregion

2.1.1. <u>Southeastern Mata Atlantica ecoregion</u>

library (FD)

library (vegan)

read.table("CoNTP.txt", header=TRUE)->CoNTP # inicial reservoir-by-species data

CoNTP

read.table("CoNFP.txt", header=TRUE)->CoNFP # initial species-by-traits data

CoNFP

functcomp(CoNFP,as.matrix(CoNTP))->CoNP # initial CWM matrix

CoNP

1-(vegdist(CoNP, method="gower"))->CoNP.d # initial similatity matrix

CoNP.d

read.table("CoNT23.txt", header=TRUE)->CoNT23 # 2002/2003 reservoir-by-species data

CoNT23

read.table("CoNF23.txt", header=TRUE)->CoNF23 # 2002/2003 species-by-traits data

CoNF23

functcomp(CoNF23,as.matrix(CoNT23))->CoN23 # 2002/2003 CWM matrix

CoN23

1-(vegdist(CoN23, method="gower"))->CoN23.d # 2002/2003 similatity matrix

CoN23.d

read.table("CoNT45.txt", header=TRUE)->CoNT45 # 2004/2005 reservoir-by-species data

CoNT45

```
read.table("CoNF45.txt", header=TRUE)->CoNF45 # 2004/2005 species-by-traits data
CoNF45
functcomp(CoNF45,as.matrix(CoNT45))->CoN45 # 2004/2005 CWM matrix
CoN45
1-(vegdist(CoN45, method="gower"))->CoN45.d # 2004/2005 similatity matrix
CoN45.d
read.table("CoNT67.txt", header=TRUE)->CoNT67 # 2006/2007 reservoir-by-species data
CoNT67
read.table("CoNF67.txt", header=TRUE)->CoNF67 # 2006/2007 species-by-traits data
CoNF67
functcomp(CoNF67,as.matrix(CoNT67))->CoN67 # 2006/2007 CWM matrix
CoN67
1-(vegdist(CoN67, method="gower"))->CoN67.d # 2006/2007 similatity matrix
CoN67.d


# Changes in pairwise functional similarities
CoN23.d-CoNP.d->deltaCoP23 # 2002/2003 similatity – initial similatity
deltaCoP23
CoN67.d-CoNP.d->deltaCoP67 # 2006/2007 similatity – initial similatity
deltaCoP67
CoN45.d- CoN23.d->deltaCoT1 # 2004/2005 similatity – 2002/2003 similatity
deltaCoT1
CoN67.d- CoN45.d->deltaCoT2 # 2006/2007 similatity – 2004/2005 similatity
deltaCoT2
```

2.1.2. <u>Iguaçu ecoregion</u>

```
library (FD)
library(vegan)
read.table("IgNTP.txt", header=TRUE)->IgNTP # inicial reservoir-by-species data
IgNTP
read.table("IgNFP.txt", header=TRUE)->IgNFP # initial species-by-traits data
IgNFP
functcomp(IgNFP,as.matrix(IgNTP))->IgNP # initial CWM matrix
IgNP
1-(vegdist(IgNP, method="gower"))->IgNP.d # initial similarity matrix
```

IgNP.d

read.table("IgNT23.txt", header=TRUE)->IgNT23 # 2002/2003 reservoir-by-species data

IgNT23

read.table("IgNF23.txt", header=TRUE)->IgNF23 # 2002/2003 species-by-traits data

IgNF23

functcomp(IgNF23,as.matrix(IgNT23))->IgN23 # 2002/2003 CWM matrix

IgN23

1-(vegdist(IgN23, method="gower"))->IgN23.d # 2002/2003 similatity matrix

IgN23.d

read.table("IgNT45.txt", header=TRUE)->IgNT45 # 2004/2005 reservoir-by-species data

IgNT45

read.table("IgNF45.txt", header=TRUE)->IgNF45 # 2004/2005 species-by-traits data

IgNF45

functcomp(IgNF45,as.matrix(IgNT45))->IgN45 # 2004/2005 similatity matrix

IgN45

1-(vegdist(IgN45, method="gower"))->IgN45.d # 2004/2005 similatity matrix

IgN45.d

read.table("IgNT67.txt", header=TRUE)->IgNT67 # 2006/2006 reservoir-by-species data

IgNT67

read.table("IgNF67.txt", header=TRUE)->IgNF67 # 2006/2007 species-by-traits data

IgNF67

functcomp(IgNF67,as.matrix(IgNT67))->IgN67 # 2006/2007 similatity matrix

IgN67

1-(vegdist(IgN67, method="gower"))->IgN67.d # 2006/2007 similatity matrix

IgN67.d

Changes in pairwise functional similarities

IgN23.d-IgNP.d->deltaIgP23 # 2002/2003 similatity – initial similatity

deltaIgP23

IgN67.d-IgNP.d->deltaIgP67 # 2006/2007 similatity – initial similatity

deltaIgP67

IgN45.d- IgN23.d->deltaIgT1 # 2004/2005 similatity – 2002/2003 similatity

deltaIgT1

IgN67.d- IgN45.d->deltaIgT2 # 2006/2007 similatity – 2004/2005 similatity

deltaIgT2

2.1.3. <u>Upper Paraná ecoregion</u>

library (FD)

library(vegan)

read.table("UpNTP.txt", header=TRUE)->UpNTP # inicial reservoir-by-species data

UpNTP

read.table("UpNFP.txt", header=TRUE)->UpNFP # initial species-by-traits data

UpNFP

functcomp(UpNFP,as.matrix(UpNTP))->UpNP # initial CWM matrix

UpNP

1-(vegdist(UpNP, method="gower"))->UpNP.d # initial similatity matrix

UpNP.d

read.table("UpNT23.txt", header=TRUE)->UpNT23 # 2002/2003 reservoir-by-species data

UpNT23

read.table("UpNF23.txt", header=TRUE)->UpNF23 # 2002/2003 species-by-traits data

UpNF23

functcomp(UpNF23,as.matrix(UpNT23))->UpN23 # 2002/2003 CWM matrix

UpN23

1-(vegdist(UpN23, method="gower"))->UpN23.d # 2002/2003 similatity matrix

UpN23.d

read.table("UpNT45.txt", header=TRUE)->UpNT45 # 2004/2005 reservoir-by-species data

UpNT45

read.table("UpNF45.txt", header=TRUE)->UpNF45 # 2004/2005 species-by-traits data

UpNF45

functcomp(UpNF45,as.matrix(UpNT45))->UpN45 # 2004/2005 CWM matrix

UpN45

1-(vegdist(UpN45, method="gower"))->UpN45.d # 2004/2005 similatity matrix

UpN45.d

read.table("UpNT67.txt", header=TRUE)->UpNT67 # 2006/2007 reservoir-by-species data

UpNT67

read.table("UpNF67.txt", header=TRUE)->UpNF67 # 2006/2007 species-by-traits data

UpNF67

functcomp(UpNF67,as.matrix(UpNT67))->UpN67 # 2006/2007 CWM matrix

UpN67

1-(vegdist(UpN67, method="gower"))->UpN67.d # 2006/2007 similatity matrix

UpN67.d

Changes in pairwise functional similarities

UpN23.d-UpNP.d->deltaUpP23 # 2002/2003 similatity – initial similatity

deltaUpP23

UpN67.d-UpNP.d->deltaUpP67 # 2006/2007 similatity – initial similatity

deltaUpP67

UpN45.d- UpN23.d->deltaUpT1 # 2004/2005 similatity – 2002/2003 similatity

deltaUpT1

UpN67.d- UpN45.d-> deltaUpT2 # 2006/2007 similatity – 2004/2005 similatity

deltaUpT2

Variation in the dispersion of the functional traits (PCoA)

3. **Inter-ecoregion**

```
library(vegan)
library(FD)
read.table("traitsP23a.txt", header=TRUE)->TP23 # 2002/2003 species-by-traits data
read.table("PAP23a.txt", header=TRUE)->PA23 # 2002/2003 reservoir-by-species data
functcomp(TP23, as.matrix(PA23))->comp4 # 2002/2003 CWM matrix
comp4
c("p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","n","n","n","n","
n","n","n","n","n","n","n","n","n","n","n","n","n","n","n","n","n","i","i","i","i","i","i","i","i","i","i","i
","i","i","i","i","i","i","i","e","e","e","e","e","e","e","e","e","e","e","e","e","e","e")->group
betadisper(gowdis(comp4),group)->res4
res4
plot(res4)
summary(res4)
res4$vectors
res4$eig # eigenvalues of the PCoA
(res4$eig/sum(res4$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res4$vectors[,1],comp4) # correlation between PCoA 1 and CWM matrix
cor(res4$vectors[,2],comp4) # correlation between PCoA 2 and CWM matrix
```

```
read.table("traitsP45a.txt", header=TRUE)->TP45 # 2004/2005 species-by-traits data
read.table("PAP45a.txt", header=TRUE)->PA45 # 2004/2005 reservoir-by-species data
functcomp(TP45, as.matrix(PA45))->comp5 # 2004/2005 CWM matrix
comp5
c("p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","n","n","n","n","
n","n","n","n","n","n","n","n","n","n","n","n","n","n","n","n","n","i","i","i","i","i","i","i","i","i","i","i
","i","i","i","i","i","i","i","i","e","e","e","e","e","e","e","e","e","e","e","e","e","e")->group
betadisper(gowdis(comp5),group)->res5
res5
plot(res5)
summary(res5)
res5$vectors
res5$eig # eigenvalues of the PCoA
(res5$eig/sum(res5$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res5$vectors[,1],comp5) # correlation between PCoA 1 and CWM matrix
cor(res5$vectors[,2],comp5) # correlation between PCoA 2 and CWM matrix


read.table("traitsP67a.txt", header=TRUE)->TP67 # 2006/2007 species-by-traits data
read.table("PAP67a.txt", header=TRUE)->PA67 # 2006/2007 reservoir-by-species data
functcomp(TP67, as.matrix(PA67))->comp6 # 2006/2007 CWM matrix
comp6
c("p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","p","n","n","n","n","
n","n","n","n","n","n","n","n","n","n","n","n","n","i","i","i","i","i","i","i","i","i","i","i","i
","i","i","i","i","i","i","e","e","e","e","e","e","e","e","e","e","e","e","e","e")->group
betadisper(gowdis(comp6),group)->res6
res6
plot(res6)
summary(res6)
res6$vectors

res6$eig # eigenvalues of the PCoA
(res6$eig/sum(res6$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res6$vectors[,1],comp6) # correlation between PCoA 1 and CWM matrix
```

cor(res6$vectors[,2],comp6) # correlation between PCoA 2 and CWM matrix

3.1. Intra-ecoregion

3.1.1. <u>Southeastern Mata Atlantica ecoregion</u>

library(vegan)

library(FD)

read.table("traitsP23.txt", header=TRUE)->TP23 # 2002/2003 species-by-traits data

read.table("PAP23.txt", header=TRUE)->PA23 # 2002/2003 reservoir-by-species data

functcomp(TP23, as.matrix(PA23))->comp4 # 2002/2003 CWM matrix

comp4

c("p","p","p","p","n","n","n","n","i","i","i","e","e","e","e")->group

betadisper(gowdis(comp4),group)->res4

res4

plot(res4)

summary(res4)

res4$vectors

res4$eig # eigenvalues of the PCoA

(res4$eig/sum(res4$eig))*100 # % of explanation

bstick(21,tot.var=1) # Broken-Stick rule

cor(res4$vectors[,1],comp4) # correlation between PCoA 1 and CWM matrix

cor(res4$vectors[,2],comp4) # correlation between PCoA 2 and CWM matrix

read.table("traitsP45.txt", header=TRUE)->TP45 # 2004/2005 species-by-traits data

read.table("PAP45.txt", header=TRUE)->PA45 # 2004/2005 reservoir-by-species data

functcomp(TP45, as.matrix(PA45))->comp5 # 2004/2005 CWM matrix

comp5

c("p","p","p","p","n","n","n","n","i","i","i","i","e","e","e","e")->group

betadisper(gowdis(comp5),group)->res5

res5

plot(res5)

summary(res5)

res5$vectors

res5$eig # eigenvalues of the PCoA

(res5$eig/sum(res5$eig))*100 # % of explanation

```
bstick(21,tot.var=1) # Broken-Stick rule
cor(res5$vectors[,1],comp5) # correlation between PCoA 1 and CWM matrix
cor(res5$vectors[,2],comp5) # correlation between PCoA 2 and CWM matrix


read.table("traitsP67.txt", header=TRUE)->TP67 # 2006/2007 species-by-traits data
read.table("PAP67.txt", header=TRUE)->PA67 # 2006/2007 reservoir-by-species data
functcomp(TP67, as.matrix(PA67))->comp6 # 2006/2007 CWM matrix
comp6
c("p","p","p","p","n","n","n","n","i","i","i","i","e","e","e","e")->group
betadisper(gowdis(comp6),group)->res6
res6
plot(res6)
summary(res6)
res6$vectors
res6$eig # eigenvalues of the PCoA
(res6$eig/sum(res6$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res6$vectors[,1],comp6) # correlation between PCoA 1 and CWM matrix
cor(res6$vectors[,2],comp6) # correlation between PCoA 2 and CWM matrix
```

3.1.2. Iguaçu ecoregion

```
library(vegan)
library(FD)
read.table("traitsP23ig.txt", header=TRUE)->TP23 # 2002/2003 species-by-traits data
read.table("PAP23ig.txt", header=TRUE)->PA23 # 2002/2003 reservoir-by-species data
functcomp(TP23, as.matrix(PA23))->comp4 # 2002/2003 CWM matrix
comp4
c("p","p","p","p","p","p","p","p","p","n","n","n","n","n","n","n","n","n","i","i","i","i","i","i","i","i","e","e","e","e","e")->group
betadisper(gowdis(comp4),group)->res4
res4
plot(res4)
summary(res4)
res4$vectors
```

```
res4$eig # eigenvalues of the PCoA
(res4$eig/sum(res4$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res4$vectors[,1],comp4) # correlation between PCoA 1 and CWM matrix
cor(res4$vectors[,2],comp4) # correlation between PCoA 2 and CWM matrix


read.table("traitsP45ig.txt", header=TRUE)->TP45 # 2004/2005 species-by-traits data
read.table("PAP45ig.txt", header=TRUE)->PA45 # 2004/2005 reservoir-by-species data
functcomp(TP45, as.matrix(PA45))->comp5 # 2004/2005 CWM matrix
comp5
c("p","p","p","p","p","p","p","p","p","n","n","n","n","n","n","n","n","n","i","i","i","i","i","i","i","
i","e","e","e","e","e")->group
betadisper(gowdis(comp5),group)->res5
res5
plot(res5)
summary(res5)
res5$vectors
res5$eig # eigenvalues of the PCoA
(res5$eig/sum(res5$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res5$vectors[,1],comp5) # correlation between PCoA 1 and CWM matrix
cor(res5$vectors[,2],comp5) # correlation between PCoA 2 and CWM matrix


read.table("traitsP67ig.txt", header=TRUE)->TP67 # 2006/2007 species-by-traits data
read.table("PAP67ig.txt", header=TRUE)->PA67 # 2006/2007 reservoir-by-species data
functcomp(TP67, as.matrix(PA67))->comp6 # 2006/2007 CWM matrix
comp6
c("p","p","p","p","p","p","p","p","p","n","n","n","n","n","n","n","n","n","i","i","i","i","i","i","i","
i","e","e","e","e","e")->group
betadisper(gowdis(comp6),group)->res6
res6
plot(res6)
summary(res6)
res6$vectors
res6$eig # eigenvalues of the PCoA
```

```
(res6$eig/sum(res6$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res6$vectors[,1],comp6) # correlation between PCoA 1 and CWM matrix
cor(res6$vectors[,2],comp6) # correlation between PCoA 2 and CWM matrix
```

3.1.3. Upper Paraná ecoregion

```
library(vegan)
library(FD)
read.table("traitsP23up.txt", header=TRUE)->TP23 # 2002/2003 species-by-traits data
read.table("PAP23up.txt", header=TRUE)->PA23 # 2002/2003 reservoir-by-species data
functcomp(TP23, as.matrix(PA23))->comp4 # 2002/2003 CWM matrix
comp4
c("p","p","p","p","p","p","p","n","n","n","n","n","n","n","i","i","i","i","i","i","i","e","e","e","e","e","e")->group
betadisper(gowdis(comp4),group)->res4
res4
plot(res4)
summary(res4)
res4$vectors
res4$eig # eigenvalues of the PCoA
(res4$eig/sum(res4$eig))*100 # % of explanation
bstick(21,tot.var=1) # Broken-Stick rule
cor(res4$vectors[,1],comp4) # correlation between PCoA 1 and CWM matrix
cor(res4$vectors[,2],comp4) # correlation between PCoA 2 and CWM matrix

read.table("traitsP45up.txt", header=TRUE)->TP45 # 2004/2005 species-by-traits data
read.table("PAP45up.txt", header=TRUE)->PA45 # 2004/2005 reservoir-by-species data
functcomp(TP45, as.matrix(PA45))->comp5 # 2004/2005 CWM matrix
comp5
c("p","p","p","p","p","p","p","n","n","n","n","n","n","n","i","i","i","i","i","i","i","e","e","e","e","e","e")->group
betadisper(gowdis(comp5),group)->res5
res5
plot(res5)
```

```
summary(res5)

res5$vectors

res5$eig # eigenvalues of the PCoA

(res5$eig/sum(res5$eig))*100 # % of explanation

bstick(21,tot.var=1) # Broken-Stick rule

cor(res5$vectors[,1],comp5) # correlation between PCoA 1 and CWM matrix

cor(res5$vectors[,2],comp5) # correlation between PCoA 2 and CWM matrix


read.table("traitsP67up.txt", header=TRUE)->TP67 # 2006/2007 species-by-traits data

read.table("PAP67up.txt", header=TRUE)->PA67 # 2006/2007 reservoir-by-species data

functcomp(TP67, as.matrix(PA67))->comp6 # 2006/2007 CWM matrix

comp6

c("p","p","p","p","p","p","p","n","n","n","n","n","n","n","i","i","i","i","i","i","i","e","e","e","e","
e","e")->group

betadisper(gowdis(comp6),group)->res6

res6

plot(res6)

summary(res6)

res6$vectors

res6$eig # eigenvalues of the PCoA

(res6$eig/sum(res6$eig))*100 # % of explanation

bstick(21,tot.var=1) # Broken-Stick rule

cor(res6$vectors[,1],comp6) # correlation between PCoA 1 and CWM matrix

cor(res6$vectors[,2],comp6) # correlation between PCoA 2 and CWM matrix
```