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3 **Introductions of non-native fishes into a heavily modified river: rates, patterns and**
4 **management issues in the Paranapanema River (Upper Paraná Ecoregion, Brazil)**

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6 Diego Azevedo Zoccal Garcia¹, John Robert Britton², Ana Paula Vidotto-Magnoni³,
7 Mário Luís Orsi³

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9 ¹Programa de Pós-Graduação em Ciências Biológicas, Universidade Estadual de
10 Londrina, Rodovia Celso Garcia Cid, Laboratório de Ecologia de Peixes e Invasões
11 Biológicas, Londrina, PR, CEP 86.057-970, Brazil

12 e-mail: diegoazgarcia@hotmail.com, Tel +55 43 3371 4477

13 ²Department of Life and Environmental Sciences, Faculty of Science and Technology,
14 Bournemouth University, Poole, Dorset. BH12 5BB, United Kingdom

15 ³Laboratório de Ecologia de Peixes e Invasões Biológicas, Universidade Estadual de
16 Londrina, Rodovia Celso Garcia Cid, Londrina, PR, CEP 86.057-970, Brazil

17

18 **Abstract**

19

20 Understanding the pathways and impacts of non-native species is important for helping
21 prevent new introductions and invasions. This is frequently challenging in regions
22 where human activities continue to promote new introductions, such as in Brazil, where
23 aquaculture and sport fishing are mainly dependent on non-native fishes. Here, the non-
24 native fish diversity of the Paranapanema River basin of the Upper Paraná River
25 Ecoregion, Brazil was quantified fully for the first time. This river has been subject to
26 considerable habitat alteration through hydroelectric dam construction and concomitant
27 development of aquaculture and sport fishing. Through compilation of a non-native fish
28 inventory by literature review, with complementary records from recent field studies,
29 analyses were completed on the timings of introduction, and the taxonomy, origin and
30 introduction vectors of the fishes. A total of 47 non-native fish are now present across
31 the basin. Of these, 24 invaded from the Lower Paraná River following construction of
32 Itaipu Dam that connected previously unconnected fish assemblages. Activities
33 including fish stocking, aquaculture and sport angling continue to result in new
34 introductions. Discounting Itaipu invasions, the introduction rate between 1950 and
35 2014 was approximately one new introduction every three years. Introduced fish were
36 mainly of the Cichlidae and Characidae families; most species were from other South
37 American ecoregions, but fishes of African, Asian, North American and Central
38 American origin were also present. These introductions have substantially modified the
39 river's fish fauna; when coupled with altered lentic conditions caused by impoundment,
40 this suggests that the river's native fishes are increasingly threatened.

41

42 **Keywords:** Biodiversity; Invasion; Aquaculture; Hydroelectric dams; Hydropower.

43

44 **Introduction**

45

46 Quantifying the extent of introductions of non-native species into different
47 biogeographic regions is important for identifying how anthropogenic activities modify
48 natural patterns of biodiversity (Villéger et al. 2011; Magurran et al. 2015). As
49 introductions of non-native species result in global biotic homogenization (Rahel 2000;
50 Olden et al. 2004), it is important to understand the pathways and rates of introductions
51 between biogeographic regions, especially in this era of globalization (Jackson and Grey
52 2013). Introductions of non-native species are often coincident with the anthropogenic
53 modification of natural habitats that can increase invasion risk (McKinney 2006; Poff et
54 al. 2007). Thus, the interaction of introduction pressure and environmental change
55 frequently exacerbates the issues faced by managers when attempting to limit new
56 introductions and then prevent invasions (Britton et al. 2011).

57

58 In freshwaters, river basins are frequently considered as biogeographic islands in which
59 opportunities for new species to invade are primarily from introductions resulting from
60 anthropogenic activities, such as aquaculture (Gozlan et al. 2010). Introduction rates
61 into river basins can be high with, for example, 96 introduced species now present in the
62 River Thames, England (Jackson and Grey 2013). In developing inventories of non-
63 native species, the identification of vectors and pathways enables identification of
64 proactive management approaches that can focus efforts on preventing further
65 introductions via greater surveillance and regulation. In some countries, pro-active
66 approaches to prevent and manage non-native species are, however, confounded by
67 environmental and societal factors that promote the likelihood of new invasions, albeit
68 often unintentionally. In Brazil, for example, a combination of measures to increase

69 hydropower provision via river impoundment, the promotion of the aquarium trade
70 using ornamental fish, and the use of intensive aquaculture is substantially increasing
71 the rate of introduction and establishment of non-native species (Britton and Orsi 2012;
72 Lima Junior et al. 2015; Xiong et al. 2015; Padial et al. 2016; Tófoli et al. 2016).
73 Indeed, there is a long legacy of introductions of non-native fishes into many Brazilian
74 river basins (Agostinho et al. 2007; Pelicice et al. 2015; Frehse et al. 2016), including
75 numerous translocations between South American ecoregions that are diverse in species
76 richness (Reis et al. 2016). Therefore, understanding the respective contributions of
77 these human activities (vectors) to the non-native fish fauna of specific Brazilian river
78 basins and ecoregions is important in determining how future introductions could be
79 prevented (Britton and Orsi 2012; Ortega et al. 2015).

80

81 The vectors responsible for the introduction of non-native freshwater fish in Brazil, in
82 areas such as the Upper Paraná freshwater ecoregion, include aquaculture (Azevedo-
83 Santos et al. 2011; Ortega et al. 2015), fish stocking to support sport angling (Britton
84 and Orsi 2012), releases of live-bait fishes used by anglers (Garcia et al. 2015), the
85 aquarium trade (Magalhães and Jacobi 2013; Magalhães and Vitule 2013), and the use
86 of fish as biological control agents (Azevedo-Santos et al. 2016). Moreover, the
87 elimination of a natural barrier to fish movement via construction of the Itaipu Dam has
88 already resulted in a mass invasion of the Upper Paraná from the Lower Paraná basin
89 (Júlio Júnior et al. 2009; Vitule et al. 2012; Daga et al. 2015). The Upper Paraná
90 ecoregion is in one of the most inventoried areas of Brazil (Graça and Pavanelli 2007;
91 Langeani et al. 2007), facilitating analysis of the origin and vectors of the non-native
92 fishes. These data then provide more precision and quality on extant knowledge of the

93 introduced species that can then be applied to developing policy and practice for their
94 management.

95

96 The Paranapanema River is a major tributary of the Upper Paraná River that has
97 undergone considerable hydro-geomorphological alteration via the construction of 11
98 hydropower reservoirs. Correspondingly, the river is a highly representative habitat in
99 South America where the interactions of human activities and environmental changes
100 are substantially altering the composition of the fish fauna. Such profound hydro-
101 geomorphological disturbances to rivers tend to promote the likelihood of invasions
102 (Johnson et al. 2008; Britton and Orsi 2012). Correspondingly, the aim here was to
103 investigate the non-native fishes that are now present in the Paranapanema River, with
104 compilation of an inventory of the species present, and analysis of their timings of
105 introduction, current distribution, origins and vectors. Their taxonomy was also
106 determined, with analysis of the orders and families of non-native fishes most
107 frequently introduced.

108

109 **Methods**

110

111 *Study area*

112 The Upper Paraná Freshwater Ecoregion is located upstream of the Itaipu Reservoir and
113 Lower Paraná River, with the Rivers Paranapanema, Grande, Paranaíba and Tietê being
114 its main tributaries (Castro et al. 2003). The ecoregion is almost entirely in Brazil,
115 except for its southwest region in Paraguay, and it is the most industrialized and
116 urbanized region of Brazil, with large number of cities with over 1 million inhabitants.
117 Originally, this area contained the Atlantic Rainforest and Brazilian Savannah biomes

118 that have now largely been converted to agriculture and livestock. In addition, the
119 Upper Paraná River basin had its watercourses transformed into reservoirs, primarily for
120 electricity production (Agostinho et al. 2007, 2016).

121

122 The Paranapanema River basin extends from the southwest of the state of São Paulo
123 (SP) to the northwest of the state of Paraná (22° - 26°S and 47 - 54°W) (Fig. 1). Its
124 sources are in the Serra de Paranapiacaba at 900 m altitude, and it flows 930 km to the
125 west before its confluence with the Paraná River. Its course is subdivided into three
126 main stretches: Upper Paranapanema, formed from the sources to the confluence of the
127 Apiaí-Guaçu River, which together with the Itapetininga River are the main tributaries
128 of this section; Middle Paranapanema, where the main tributaries are Itararé and Pardo
129 rivers; and Lower Paranapanema, with the Rivers Cinzas, Tibagi and Pirapó being the
130 main tributaries (Sampaio 1944) (Fig. 1). The hydroelectric development of the
131 Paranapanema River began in 1936, with 11 dams now present that have modified the
132 main river channel into a succession of cascading reservoirs (Fig. 1; Orsi et al. 2016).
133 Cage and tank aquaculture is practised in and around some reservoirs (Orsi and
134 Agostinho 1999; Ramos et al. 2013). The naturally high fish species richness of the
135 basin (127 species, e.g. Castro et al. 2003; Duke Energy 2008) is threatened by these
136 reservoirs, with considerable declines in native fish species richness being recorded in,
137 for example, the Capivara Reservoir (Orsi and Britton 2014). For the purposes of this
138 study, the presence of non-native fishes within the basin was considered across 11
139 locations that covered the major hydroelectric reservoirs, the main river channel and
140 river tributaries (Fig. 1; Table1).

141

142

143 *Fish species inventory and data analysis*

144 In the study, a species was considered to be non-native in the Paranapanema River if
145 literature suggested it should not have naturally occurred in the river due to
146 biogeographical factors. The non-native fishes in the river thus included species from
147 other ecoregions of South America, as well as from other continents. They also included
148 species from the Lower Paraná River that, prior to construction of the Itaipu Dam, were
149 biogeographically isolated from the Upper Paraná River (Vitule et al. 2012).

150

151 To compile the inventory list of non-native fishes, the principal method was literature
152 review. The review was based on searches completed in Web of Science, and
153 supplemented by Google Scholar, starting with the river name ('Paranapanema') or
154 ecoregion ('Upper Paraná') in 'title' searches, and then using these within Boolean logic
155 search terms with words including 'alien', 'non-native', 'invasive', 'non-indigenous',
156 'introduced', 'allodiversity', and their combinations. Searches were then completed
157 using the same terms but searching for 'topic' to provide any additional material that
158 would otherwise have been missed. These searches provided an overall list of literature
159 that, following review, provided a reduced number of papers from which information
160 relevant to the study were extracted. In addition to these published sources, grey
161 literature was also sourced. This grey literature primarily comprised documents
162 published by power companies in charge of the hydroelectric dams and often provided
163 details on intentional introductions of non-native fish into the reservoirs that were not
164 available from any other source (e.g. CESP 1997). This review thus provided a list of
165 non-native fishes that have been introduced into the Paranapanema River. Some of the
166 papers and reports also provided complementary information on the timing of detection
167 of the non-native fish (and their introduction in some cases), plus their taxonomy, native

168 origin and introduction vector. Where taxonomic and native origin information was not
169 available then it was collated from other literature sources; these were primarily Reis et
170 al. (2003), Britski et al. (2007), and Eschmeyer et al. (2016).

171

172 The introduction vector of each species was assessed from information provided in the
173 original literature source; when this information was not present, then the vector was
174 interpreted from subsequent literature on that species (e.g. whether it is primarily a
175 species used in aquaculture or sport angling). Where this information was lacking then
176 author knowledge was used. The vectors that were identified were: (i) fish stocking via
177 sport-angling; (ii) live-bait fishes used in sport angling; (iii) aquaculture ('fish
178 farming'); (iv) biological control (primarily of mosquito); (v) Itaipu Dam, where the
179 non-native fish was present in the river only as a direct consequence of their upstream
180 movement that was enabled by the dam flooding the natural biogeographic barrier of the
181 Sete Quedas Falls; and (vi) the aquarium trade (Júlio Júnior et al. 2009; Britton and Orsi
182 2012; Vitule et al. 2012; Azevedo-Santos et al. 2016).

183

184 To provide an up-to-date inventory of non-native species in the river, the literature
185 review was complemented by field samples. These samples had been collected quarterly
186 between 2012 and 2014 as part of a monitoring project within the Paranapanema River
187 basin to detect natural fish spawning and nursery areas. Data from these samples were
188 used here only to provide new information on the presence of non-native fishes that
189 represented a new introduction as they had yet to be reported in the literature. The
190 samples were collected from the major habitats of the Rosana, Taquaruçu, Capivara,
191 Canoas I, Canoas II and Salto Grande reservoirs, and their river tributaries (Fig. 1).
192 Adult and juvenile fishes were captured by seine nets (6.0 m², 2.0 mm of mesh) and

193 complemented by samples of juvenile and larval fishes collected by sieves (0.4 m², 0.5
194 mm of mesh). As any identified new species would have no supporting information on
195 their native origin and vector, these were determined through literature review and
196 author opinion, as described above.

197

198 Following compilation of the inventory list of the non-native fishes and their associated
199 information (taxonomy, timing of introduction, native origin, and vector), these data
200 were evaluated to determine their main patterns. To assess the temporal and spatial
201 pattern of non-native fish introductions, the year of their first detection/introduction was
202 identified (where detection was used as a proxy of the year of introduction). This
203 enabled calculation of the proportion of non-native species that were introduced over
204 time, their introduction rate per year, the cumulative number present, and the spatial
205 variation in the number of species present in the different reservoirs (Fig. 1). If the
206 introduced species was South American, then their geographic origin was given as the
207 donor freshwater ecoregion (Abell et al. 2008); if its origin was from outside of South
208 America then their continent was used (e.g. Africa, Asia, North America and Central
209 America). Analysis of the vectors of introduction was determined as the proportion of
210 species that were introduced via that vector. In addition, information on fish stockings
211 rates in the reservoirs was provided where this was available. Note that the species lists
212 and associated information used in these analyses are provided in full in Appendices 1
213 and 2 of the Supplementary Material.

214

215

216

217

218 **Results**

219

220 *Literature review*

221 Initial searches of the river and ecoregion names were used to identify the temporal
222 pattern in the literature of the region. ‘Paranapanema’ returned 86 papers in Web of
223 Science, published between 1992 and 2017, of which 58 (67 %) have been published in
224 the last decade (taken as 2008 to 2017). ‘Upper Paraná’ returned 328 papers in Web of
225 Science, published between 1968 and 2017, of which 208 (63 %) have been published
226 in the last decade. Of these peer-reviewed papers, information on the introduced fishes
227 of the Paranapanema River basin was extracted from 20. This information was then
228 supplemented by searched in Google Scholar that provided a further 10 papers in non-
229 ISI journals from which information was extracted. Finally, a combination of online
230 searches and sourced documents from power companies (e.g. providing stocking
231 records) and universities (e.g. PhD theses) provided a further 15 literature sources from
232 which data were extracted. Thus, the literature review aspect of the study is based on 30
233 peer-reviewed papers and 15 items of grey literature (*cf.* Supplementary Material).

234

235 *Initial non-native fish introductions*

236 Literature review revealed that the first recorded non-native fish in the Paranapanema
237 River occurred in the 1950s, with the North American largemouth bass, *Micropterus*
238 *salmoides* Lacepède, 1802, reported (Fig. 2; Appendix 2). Further deliberate
239 introductions of non-native fishes occurred between 1978 and 1992 through fish
240 stocking programmes conducted by ‘Companhia Energética de São Paulo’ (CESP
241 1997), with seven non-native species released (Table 1; Appendix 2). A major
242 introduction event was then the flooding of the natural biogeographic barrier of the Sete

243 Quedas Falls during the formation of the Itaipu Reservoir. This enabled 24 fishes
244 originating from the Lower Paraná Ecoregion to disperse upstream into the
245 Paranapanema River (Júlio Júnior et al. 2009; Vitule et al. 2012; Daga et al. 2015), with
246 these new species resulting in a major peak in the introduction rate (Fig. 2).

247

248 *Non-native fish composition and distribution*

249 A total of 45 non-native fish species have been recorded in the literature as being
250 introduced into the Paranapanema River between 1950 and 2014 (Table 2; Appendix 1).
251 The field sampling conducted between 2012 and 2014 in a number of reservoirs and
252 their tributaries (*cf.* Methods) increased this total to 47 non-native fishes (Table 2;
253 Appendix 1). This represents an overall rate of 0.72 new species per year; if the 24
254 fishes associated with the construction of the Itaipu Dam are removed from the data
255 then this reduces to 0.35 new species per year. The 47 non-native fishes belong to eight
256 orders and 21 families. The orders are primarily Characiformes (8 families, 13 species),
257 Siluriformes (6 families, 12 species), and Perciformes (3 families, 12 species)
258 (Appendix 1).

259

260 The two new non-native fishes added to the non-native fish inventory from the field
261 sampling were *Ossancora eigenmanni* (Boulenger, 1895) and *Laetacara araguaiae*
262 Ottoni & Costa, 2009. Note that although *O. eigenmanni* has previously been recorded
263 in the basin, it had only been recorded as unidentified Doradidae (Duke Energy 2008),
264 with these new samples now enabling their identification to species level. Conversely,
265 *L. araguaiae* has not reported previously but was present in field samples collected
266 from the Rosana Reservoir in 2013 and was subsequently identified to species level in
267 the laboratory.

268 Information gathered from the published literature revealed that in terms of distribution
269 in the Paranapanema River, the species that have been detected in at least 9 of the 11
270 evaluated habitats of the basin were *Hyphesobrycon eques* (Steindachner, 1882) (mato-
271 grosso), *Metynnis lippincottianus* (Cope, 1870) (pacu-cd), *Plagioscion squamosissimus*
272 Heckel, 1840 (corvina), and *Oreochromis niloticus* (Linnaeus, 1758) (Nile tilapia) (Fig.
273 1; Table 2; Appendix 1). Most of the non-native fishes were recorded within the
274 hydropower reservoirs, whereas only a small proportion were recorded as being present
275 in the main river channel (Fig. 3). Of the reservoirs, the Rosana, Taquaruçu, and
276 Capivara reservoirs had the highest numbers of introduced non-native fishes (Fig. 3).

277

278 *Native origin and vectors*

279 Nine South American freshwater ecoregions provided 38 of the 47 non-native fishes
280 present in the basin (83% of all introductions) (Fig. 4a). The regions of native origin of
281 these species were primarily Paraguay and the Lower Paraná ecoregions, the Amazonas,
282 Orinoco, Guianas, and Uruguay River basins. The importance of the Lower Paraná
283 ecoregion as a donor region is reflected in the main introduction vector being the
284 flooding of the Sete Quedas Falls via Itaipu Dam construction that enabled 24 species to
285 invade (Fig. 4b). The native origins of species outside of South America were Africa,
286 Asia, North America and Central America, with their vectors mainly being aquaculture,
287 fish stocking and release of ornamental fish (aquarium trade) (Fig. 4b).

288

289 **Discussion**

290

291 The number of non-native fishes in the reservoirs and tributaries of the Paranapanema
292 River basin of the Upper Paraná Ecoregion has continued to increase over time, with at

293 least 47 non-native fishes now present. When the influence of the Itaipu Dam is
294 removed from the data, there was a new fish species recorded in the river approximately
295 every three years. These results represent the highest numbers of non-native fish
296 recorded in the Paranapanema River basin to date. In the riverine habitats, three non-
297 native fishes have been recorded previously (Castro et al. 2003), whereas in reservoirs
298 and the tributaries, previous recordings were 13 species (Carvalho et al. 2005) through
299 to 27 (Orsi et al. 2016), 31 (Duke Energy 2008), and finally up to 39 species (Ortega et
300 al. 2015). The families now contributing most to the introduced fish fauna are the
301 Cichlidae and Characidae; of the 10 cichlids present, five have been recorded as *Cichla*
302 spp. (peacock basses).

303

304 Across the wider literature review, it was apparent that the Paranapanema River has a
305 relatively low native fish species richness compared to other rivers of the Upper Paraná
306 Ecoregion (e.g. compared to the Paraná, Paranaíba, Grande and Tietê rivers) (Agostinho
307 et al. 1997). However, it was also apparent that the Paranapanema now has a relatively
308 high number of introduced fishes compared with some of these other rivers (Ortega et
309 al. 2015). In other areas of the world that have been studied for their non-native taxa, 15
310 non-native fish species were recently recorded in the River Thames, England (of 96
311 non-native species recorded in total) (Jackson and Grey 2013) and in Lake Naivasha,
312 Kenya, 11 non-native fish were introduced between the 1920s and 2000s (Gherardi et
313 al. 2011). Kolar and Lodge (2002) identified 45 non-native fishes in the North
314 American Great Lakes for development of their invasion predictions and risk
315 assessment. As each of these freshwater systems were described as highly invaded
316 (Kolar and Lodge, 2002; Gherardi et al. 2011; Jackson and Grey 2013) then the

317 Paranapanema River can thus also be considered as a highly invaded freshwater system
318 at the global scale.

319

320 The construction of the Itaipu Dam was responsible for over 50% of the non-native fish
321 present in the Paranapanema River basin. The construction of this dam flooded the Sete
322 Quedas Falls in 1982 that comprised of a sequence of 19 groups of waterfalls that
323 physically separated the fish fauna of Upper and Lower Paraná basins (Bonetto 1986;
324 Vitule et al. 2012). Its flooding enabled the upstream dispersal of a number of fishes
325 from the Lower Paraná basin into the Upper Paraná basin where they were non-
326 indigenous (Júlio Júnior et al. 2009). The movement of these fishes through the
327 Paranapanema River was restricted by the Capivara Dam that was built in 1978 without
328 fish passage. However, species such as *Pterygoplichthys ambrosettii* (Holmberg, 1893)
329 and *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 have since moved above
330 this dam following their rescue from its hydropower turbines and their subsequent
331 translocation into the upstream reservoir (Casimiro et al. 2017). In addition, the 11
332 hydroelectric reservoirs now present dam along the Paranapanema River have enabled
333 increased cage aquaculture and the creation of sport fisheries (Britton and Orsi 2012).
334 Both activities are heavily reliant on non-native fishes such as *O. niloticus* and *Cichla*
335 spp. respectively (Britton and Orsi 2012). In addition, at least 13 million fish across
336 seven non-native species were released in the reservoirs in stocking events between
337 1978 and 1992, with these fishes now having established populations (CESP 1997).
338 This number of released fishes could be considered as representing high propagule
339 pressure, an important factor that tends to increase the probability of introduced species
340 establishing (Lockwood et al. 2005, 2009). It is thus suggested that the major
341 engineering of the Paranapanema basin specifically, and the Paraná River more

342 generally, has been the primary driver for the increased non-native fish diversity, and
343 thus all other introduction vectors may be considered secondary and/or supplementary
344 to this.

345

346 Although this study has documented 47 introduced fish in the basin, the invasion status
347 of these fish (for example, whether they are established or invasive) was not always
348 apparent. However, with their repeated reporting in the literature and/or their recording
349 in field samples, it was apparent that most of these fishes have, at the very least,
350 established sustainable populations. The high proportion of these fishes within the
351 reservoirs, rather than the main river channel, suggests that these are important habitats
352 for the establishment of these fishes. Indeed, studies generally suggest that
353 impoundments enhance the probability of non-native fishes establishing populations
354 (e.g. Johnson et al. 2008). The high proportion of invasive cichlids in the Paranapanema
355 reservoirs is also supported by other studies that suggest Neotropical impoundments are
356 prone to dominance by introduced cichlids (e.g. Agostinho et al. 2007; Langeani et al.
357 2007; Ortega et al. 2015). The dominance of cichlid fishes, such as *Cichla*, in the altered
358 hydro-geomorphic conditions of the reservoirs might also relate to the shift in abiotic
359 conditions in the reservoirs, for example, their reduced turbidity. This is because
360 increased water clarity can assist sight feeding piscivores in prey detection and capture,
361 even in the presence of macrophytes that usually provide prey refugia (Pelicice and
362 Agostinho 2009). A potentially important factor in the establishment of *Cichla* spp. in
363 the reservoirs is also their reproductive plasticity. The spawning of *Cichla piquiti*
364 Kullander & Ferreira, 2006 is seasonal in their native Amazonian rivers, with increased
365 reproductive activity at the beginning of the rainy season (Muñoz et al., 2006). In their
366 invasive population of the Itumbiara Reservoir (Paranaíba River basin, Southeast

367 Brazil), however, reproduction occurred throughout the year (Vieira et al. 2009). This
368 shift in reproductive behaviour, that was asynchronous with rainfall and peak water
369 temperatures, potentially conferred considerable invasion advantages via elevated
370 recruitment (Vieira et al. 2009). Plasticity in life history traits is a feature of many
371 successful invaders, as it usually enables rapid adaptive responses to new conditions
372 (Gozlan et al. 2010). For example, demographic bottlenecks relating to low founding
373 population sizes can be overcome through the introduced individuals growing faster and
374 maturing earlier in order to be able to establish populations more rapidly (Britton and
375 Gozlan 2013).

376

377 The high number of non-native fishes introduced into the Paranapanema River means it
378 is important to consider their ecological impacts, especially as the river also has a
379 relatively high native fish species richness at global levels (at least 127 fishes; Castro et
380 al. 2003; Duke Energy 2008). In the reservoirs, there has been an increased number and
381 abundance of invasive piscivorous fishes, especially of the *Cichla* genus (Orsi and
382 Britton 2014). The impacts of introduced *Cichla* fishes have already received
383 considerable attention in the Paraná basin more generally, where they have reportedly
384 substantially increased predation pressure, resulting in deleterious impacts on native fish
385 species richness (e.g. Pelicice and Agostinho 2009; Menezes et al. 2012; Pelicice et al.
386 2015). A study documenting temporal changes in the fish assemblage of the Capivara
387 Reservoir between 1992 and 2010 revealed that of 50 native fishes present in the initial
388 samples, there were only 23 present in final samples, with an additional 11 non-native
389 fish by 2010 (Orsi and Britton 2014). However, as this native diversity started to
390 decrease prior to *Cichla* establishment, then it was most likely driven initially by the

391 substantial alterations to the hydro-geomorphology of the river, with losses then
392 exacerbated by high *Cichla* predation pressure (Orsi and Britton 2014).

393

394 The importance of vectors such as the Itaipu Dam for non-native fish introductions in
395 the Paranapanema River was reflected in the origin of most introduced fishes being
396 other Neotropical basins and South American ecoregions. Indeed, this is typical of the
397 non-native fish fauna of Neotropical reservoirs more generally (Ortega et al. 2015;
398 Latini et al. 2016). However, non-native fishes were also present in the Paranapanema
399 River from four other continents, revealing how globalization of activities such as the
400 ornamental fish trade and aquaculture has resulted in some fishes, such as *Cyprinus*
401 *carpio* Linnaeus, 1758 and *O. niloticus*, achieving a worldwide distribution (Gozlan et
402 al. 2010; Britton and Gozlan 2013). Moreover, given the propensity of fish farmers to
403 diversify their cultured fishes using fish from different countries and continents (Gozlan
404 2008), it is probable that more non-South American fish will be introduced into the
405 Paranapanema basin via aquaculture in future.

406

407 From a management perspective, the increased non-native fish diversity and decrease in
408 native diversity in the Paranapanema River basin raises substantial conservation
409 concerns. These results suggest that strategies that prevent new introductions via better
410 regulation of the important introduction vectors should be considered. For example, the
411 aquaculture sector is an important economic activity in the Paranapanema basin and is
412 an important introduction vector in the Upper Paraná ecoregion (Agostinho et al. 2007;
413 Ortega et al. 2015; Latini et al. 2016). Non-native fishes, including *Clarias gariepinus*
414 (Burchell, 1822) and *O. niloticus* are cultured (Orsi and Agostinho 1999); both are
415 global invaders and harmful to native fish diversity (Forneck et al. 2016; Latini et al.

416 2016; Padial et al. 2016). Brazilian aquaculture also tends to prefer cultivating non-
417 native species (Agostinho et al. 2007), with a proposed bill (Law 5989/09) encouraging
418 this further (e.g. Pelicice et al. 2014). In combination, this suggests there is a pressing
419 requirement for increased education of fish farmers on the risks their activities can pose
420 to native fish diversity. This should be allied with enhanced biosecurity of aquaculture
421 sites to prevent fish escapes, with a concomitant shift towards farming native fishes
422 (Britton and Orsi 2012; Forneck et al. 2016). It is also recommended that all policies
423 that promote introducing non-native fishes in reservoirs (e.g. for sport angling) are
424 terminated, with increased regulation and supervision on the keeping and release of
425 ornamental fishes by the public. Unfortunately, given the large spatial distribution of
426 many of the extant non-native fishes that have been introduced into the Paranapanema
427 River basin, there are few management options available that would be effective at
428 preventing their further dispersal and impact (Britton et al. 2011). Consequently,
429 management priorities could aim to prevent new introductions and implement
430 mitigation actions that protect native fish diversity.

431

432 In summary, the Paranapanema River is a highly altered river system due to the
433 construction of hydroelectric reservoirs. These altered conditions, in conjunction with
434 human activities such as aquaculture and sport angling, have facilitated the introduction
435 and subsequent invasion of many non-native fishes. Thus, it is apparent that the fish
436 fauna of this river within the Upper Paraná Ecoregion has been heavily modified due to
437 a range of human activities that have altered its physical and biological characteristics,
438 and facilitated the introduction and invasion of many non-native fishes.

439

440

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442

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447

448 **References**

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626

Table 1 Number of individuals of non-native fish species stocked in reservoirs of the Paranapanema River between 1978 and 1992, from stocking programs conducted by ‘Companhia Energética de São Paulo’ (CESP 1997).

Species	Reservoir					Total
	Rosana	Capivara	Salto Grande	Chavantes	Jurumirim	
<i>Astronotus crassipinnis</i>	0	26,300	34,000	17,000	24,000	101,300
<i>Cyprinus carpio</i>	0	390,000	135,000	265,646	819,557	1,610,203
<i>Sorubim lima</i>	10,000	9,000	0	0	0	19,000
<i>Schizodon borellii</i>	0	30,000	38,000	60,144	90,000	218,144
<i>Triportheus angulatus</i>	0	1,075,000	52,642	80,000	305,000	1,512,642
<i>Oreochromis niloticus</i>	0	1,935,000	615,000	1,243,000	5,694,200	9,487,200
<i>Hoplias lacerdae</i>	0	188,280	27,800	50,000	169,300	435,380
Total	10,000	3,653,580	902,442	1,715,790	7,102,057	13,383,869

Table 2 Composition and distribution of the non-native fish species introduced into the Paranapanema River basin between 1950 and 2014, where ‘X’ denotes introduced and ‘-’ denotes absence in that location. Locations are shown in Fig. 1 and are represented here as: Ros = Rosana Reservoir; Taq = Taquaruçu Reservoir; Cap = Capivara Reservoir; Tib = Tibagi River; Can I = Canoas I Reservoir; Can II = Canoas II Reservoir; Sgr = Salto Grande Reservoir; Our = Ourinhos Fish Ladder; Cha = Chavantes Reservoir; Jur = Jurumirim Reservoir; Upper = Tributaries of the Upper Paranapanema River. For taxonomic details by species and the sources of information on the introduction, please see Appendix 1 of Supplementary Material.

Species	Location within the Paranapanema River basin										
	Ros	Taq	Cap	Tib	Can I	Can II	Sgr	Our	Cha	Jur	Upper
<i>Aphyocharax dentatus</i>	X	X	X	-	X	X	-	-	-	-	-
<i>Apteronotus caudimaculosus</i>	-	-	X	-	-	-	-	-	-	-	-
<i>Astronotus crassipinnis</i>	X	-	X	-	X	X	X	X	-	-	-
<i>Auchenipterus osteomystax</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Brachyhypopomus pinnicaudatus</i>	-	-	-	-	-	-	X	-	-	-	-
<i>Bryconamericus exodon</i>	-	-	-	X	-	-	-	-	-	-	-
<i>Catathyridium jenynsii</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Cichla kelberi</i>	X	-	X	-	-	-	X	-	X	-	-
<i>Cichla monoculus</i>	-	-	X	-	X	X	-	-	-	X	-
<i>Cichla ocellaris</i>	-	-	-	-	-	-	-	X	-	-	-

<i>Cichla piquiti</i>	-	-	-	-	-	-	-	X	-	X	-	-
<i>Cichla temensis</i>	-	-	-	-	-	-	-	-	X	-	-	-
<i>Clarias gariepinus</i>	-	X	X	X	-	-	-	-	-	-	-	-
<i>Coptodon rendalli</i>	X	-	X	X	-	-	-	-	X	-	X	-
<i>Ctenopharyngodon idella</i>	-	-	-	X	-	-	-	-	-	-	-	-
<i>Cyprinus carpio</i>	-	-	X	X	-	-	-	-	-	-	X	X
<i>Erythrinus erythrinus</i>	X	-	X	-	-	-	-	-	-	-	-	-
<i>Hoplias lacerdae</i>	-	-	-	-	-	-	-	-	-	-	X	-
<i>Hyphessobrycon eques</i>	X	X	X	X	X	X	X	X	X	-	X	-
<i>Hypophthalmus edentatus</i>	X	X	-	-	-	-	-	-	-	-	-	-
<i>Ictalurus punctatus</i>	-	-	X	-	-	-	-	-	-	X	-	-
<i>Laetacara araguaiae</i>	X	-	-	-	-	-	-	-	-	-	-	-
<i>Leporinus macrocephalus</i>	-	-	X	X	X	-	X	-	-	-	-	-
<i>Loricariichthys platymetopon</i>	X	X	X	X	X	X	-	-	-	-	-	-
<i>Metynnis lippincottianus</i>	X	X	X	X	X	X	X	-	-	-	X	-
<i>Micropterus salmoides</i>	-	-	-	X	-	-	-	-	-	-	-	-
<i>Misgurnus anguillicaudatus</i>	-	-	-	-	-	-	-	-	-	-	-	X
<i>Oreochromis niloticus</i>	X	X	X	X	X	X	X	-	X	X	X	X
<i>Ossancora eigenmanni</i>	X	X	-	-	-	-	-	-	-	-	-	-
<i>Pimelodus ornatus</i>	X	X	-	-	-	-	-	-	-	-	-	-

<i>Plagioscion squamosissimus</i>	X	X	X	X	X	X	X	X	X	-	-
<i>Poecilia reticulata</i>	X	X	X	X	-	-	X	X	-	-	-
<i>Potamotrygon cf. motoro</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Pterodoras granulosus</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Pterygoplichthys ambrosettii</i>	X	-	X	-	-	-	-	-	-	-	-
<i>Rhamphichthys hahni</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Roeboides descavadensis</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Satanoperca pappaterra</i>	X	-	-	-	-	-	-	-	-	-	-
<i>Schizodon borellii</i>	X	X	X	-	-	-	-	-	-	-	-
<i>Serrasalmus marginatus</i>	X	X	-	-	-	-	-	-	X	-	-
<i>Sorubim lima</i>	X	X	X	X	-	X	-	-	-	-	-
<i>Steindachnerina brevipinna</i>	X	-	-	-	-	-	-	-	-	-	-
<i>Trachelyopterus galeatus</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Trachydoras paraguayensis</i>	X	X	-	-	-	-	-	-	-	-	-
<i>Triportheus angulatus</i>	-	-	X	X	-	-	-	-	-	-	-
<i>Triportheus nematurus</i>	-	X	X	-	-	-	X	-	X	X	-
<i>Xiphophorus hellerii</i>	X	-	-	-	-	-	-	-	X	-	-
Total number of species by location	30	23	22	15	9	9	11	7	8	8	3

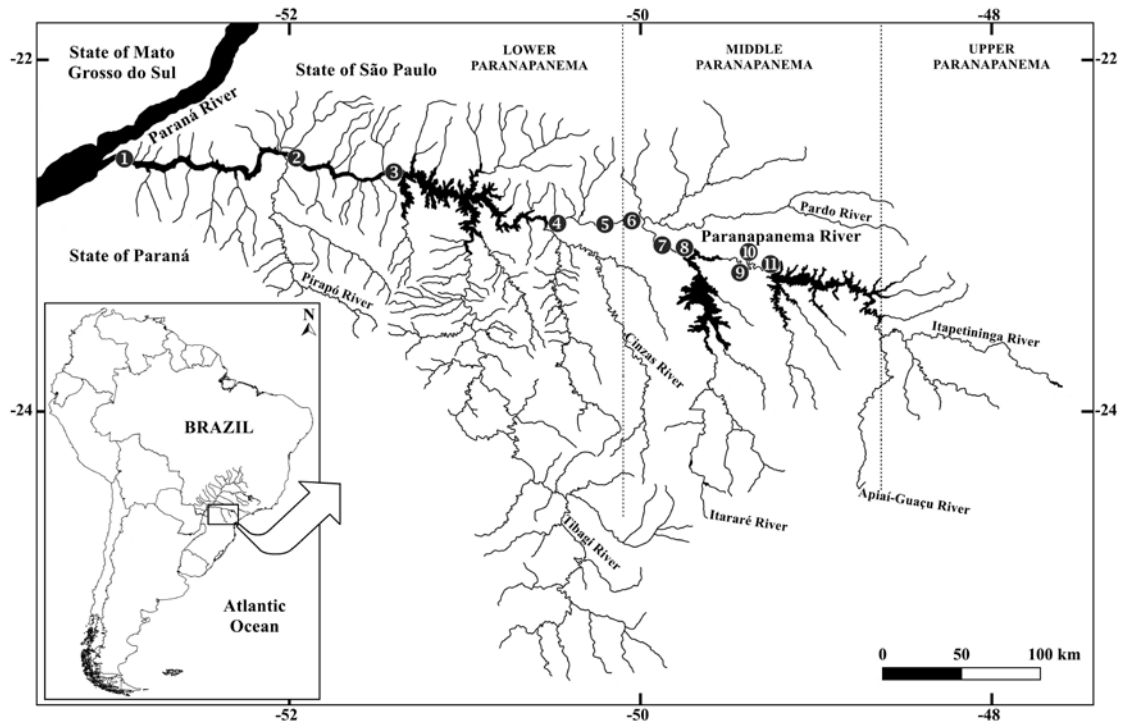


Fig. 1 Inset: Location of the study area in Brazil. Main: the Paranapanema River basin located in the Upper Paraná Ecoregion, where the numbers represent the locations of the hydroelectric reservoirs: 1) Rosana; 2) Taquaruçu; 3) Capivara; 4) Canoas I; 5) Canoas II; 6) Salto Grande; 7) Ourinhos; 8) Chavantes; 9) Paranapanema; 10) Piraju; and 11) Jurumirim.

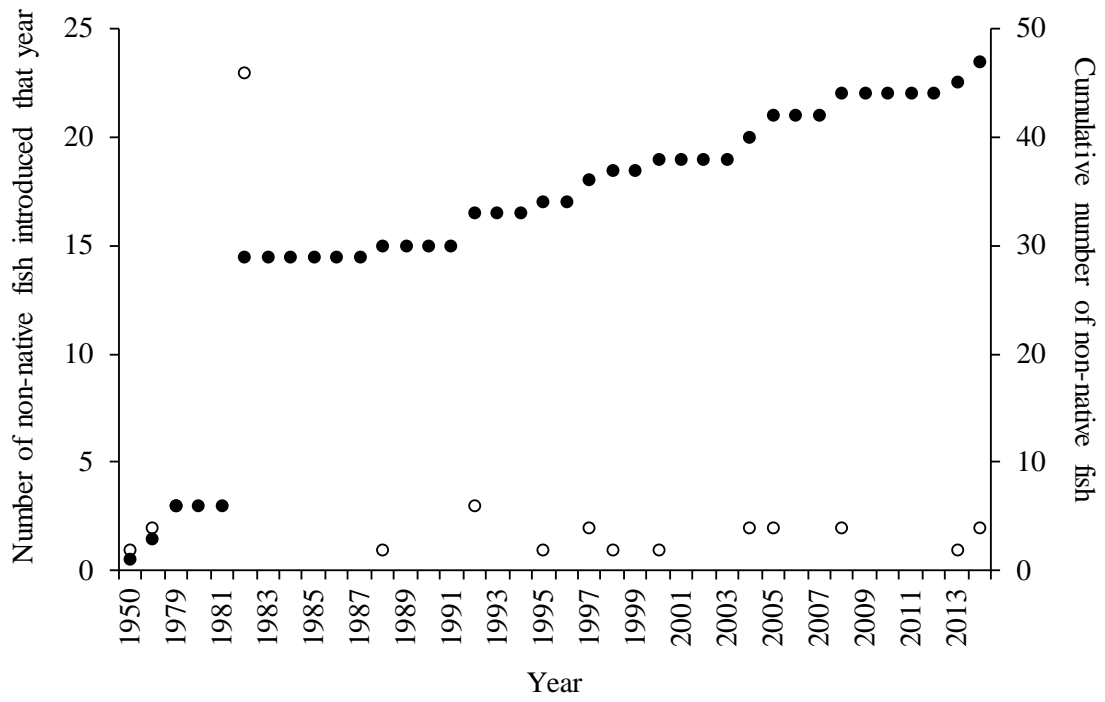


Fig. 2 Number of non-native fish species introduced in the Paranapanema River basin per year between 1950 and 2014 (clear circles) and the cumulative number of non-native fishes that have been introduced (filled circles).

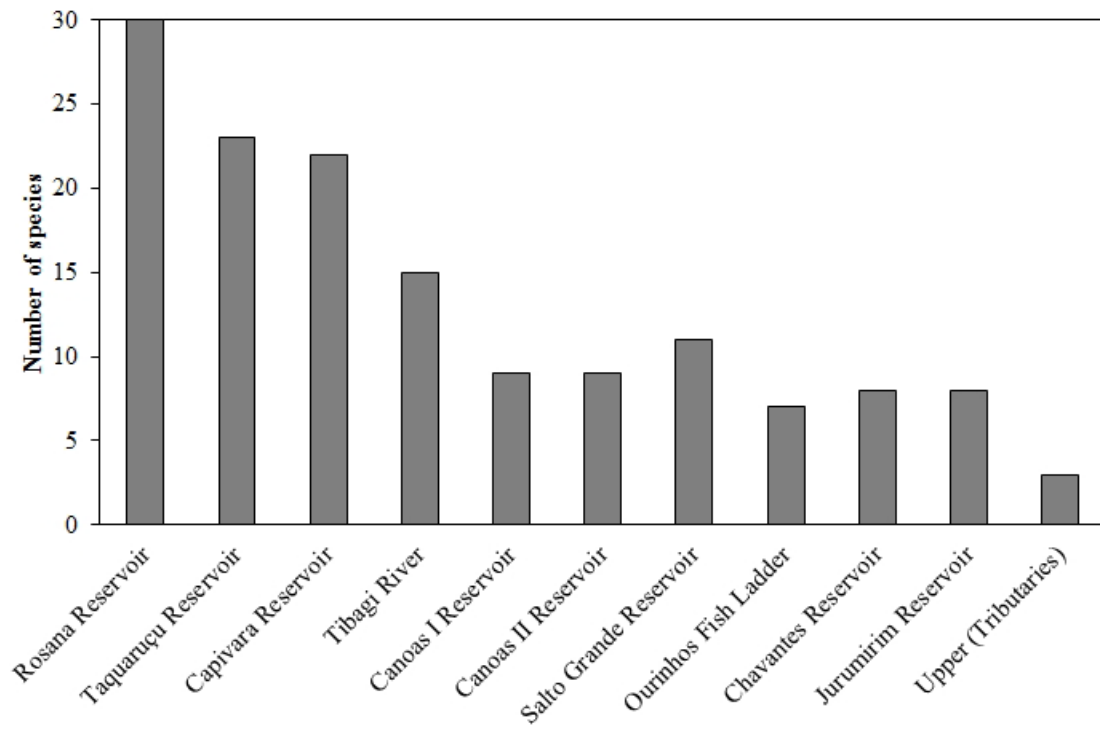


Fig. 3 The number of non-native fish present in each hydroelectric reservoir and river tributary of in the Paranapanema River basin. Information gathered from literature and field samples.

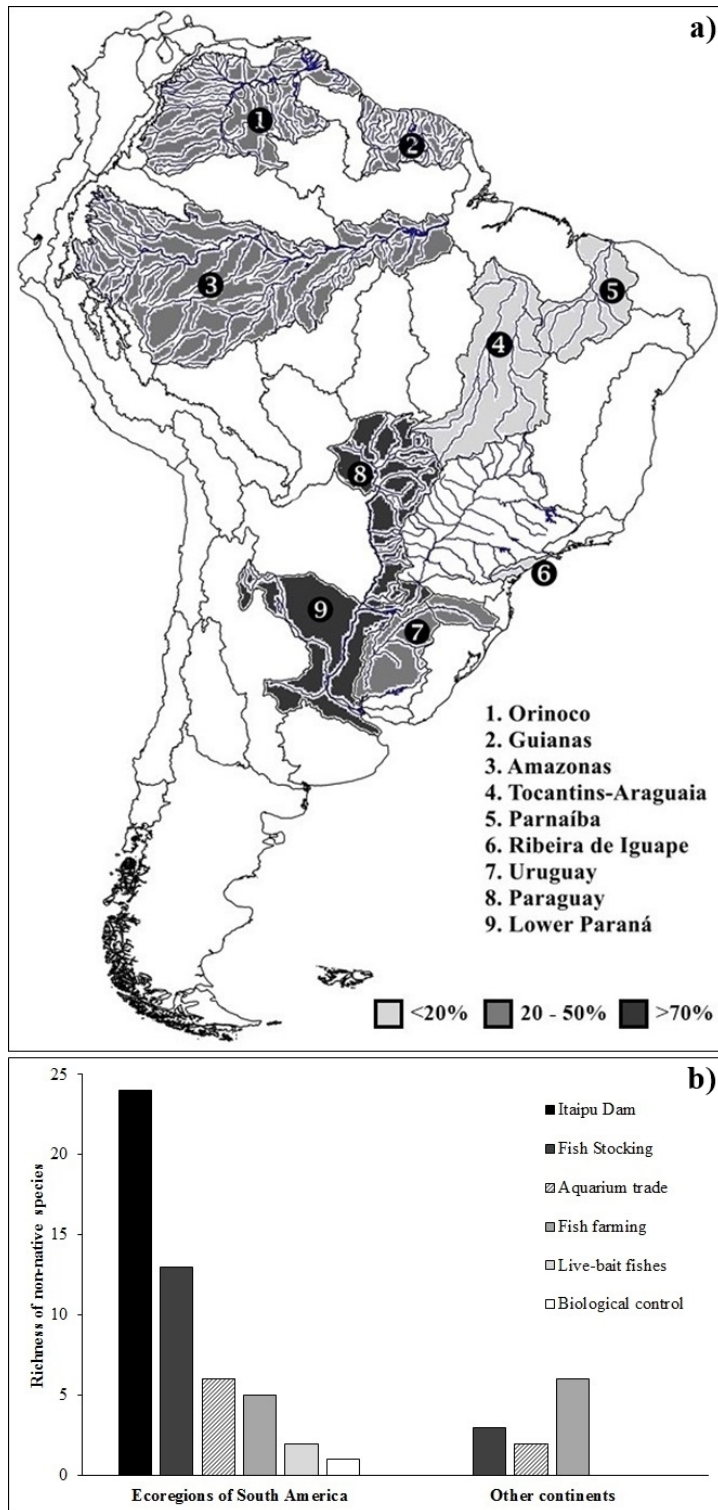


Fig. 4 (a) Origin of the non-native fish species (N = 47) introduced into the Paranapanema River according to South American ecoregions (Abell et al. 2008); (b) Origins of the non-native fish species introduced into the Paranapanema River according to the vector of introduction.