



HAL
open science

Important characteristics determining the success of nonnative freshwater fish introduction, establishment, and impact.

Camille Bernery, Céline Bellard, Franck Courchamp, Sébastien Brosse, Boris Leroy

► To cite this version:

Camille Bernery, Céline Bellard, Franck Courchamp, Sébastien Brosse, Boris Leroy. Important characteristics determining the success of nonnative freshwater fish introduction, establishment, and impact.. 2022. hal-03563547

HAL Id: hal-03563547

<https://hal.science/hal-03563547>

Preprint submitted on 9 Feb 2022

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

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

1 **Important characteristics determining the success of non-native**
2 **freshwater fish introduction, establishment, and impact.**

3 **Running title : Characteristics of successful fish invaders**
4
5

6 Camille Bernery^{1*}, Céline Bellard¹, Franck Courchamp¹, Sébastien Brosse², Boris Leroy³

7 ¹ Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405,
8 Orsay, France

9 ² Laboratoire Évolution & Diversité Biologique (EDB UMR5174), Université Paul Sabatier -
10 Toulouse 3, CNRS, IRD, UPS, 118 route de Narbonne, 31062 Toulouse Cedex, France

11 ³ Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA UMR 7208), Muséum
12 National d'Histoire Naturelle, Sorbonne Universités, Université de Caen Normandie, Université
13 des Antilles, CNRS, IRD, Paris, France

14 * corresponding author: Camille.bernery@universite-paris-saclay.fr
15

16 **Abstract**

17 **Aim**

18 The invasion success of introduced freshwater fish is influenced by many factors, including
19 ecological, species, and socioeconomic characteristics. Most studies that document the
20 importance of one of these factors are conducted at a local scale and/or focus on a single step
21 of the invasion process. Here, our aim is to identify the characteristics of successful invaders
22 across the entire invasion process using ecological, species, and socioeconomic characteristics.

23 **Location**

24 Worldwide.

25 **Time period**

26 Contemporary.

27 **Major taxa studied**

28 Freshwater fish.

29 **Methods**

30 We conducted a worldwide analysis of 307 freshwater fish species and considered the number
31 of countries in which each species was introduced, established, or had ecological impacts as a
32 proxy of invasion step success. We applied generalized linear models to 20 variables relating
33 to species morphology, ecology, and introduction pathways to determine the main
34 characteristics associated with invasion success. By disentangling our results by pathways, we
35 specifically explore the role played by aquaculture and ornamental trade pathways in the
36 characteristic selection.

37 **Results**

38 We found that non-native freshwater fish with a broad diet, high parental care, and multiple
39 introduction pathways are the most widely introduced and established worldwide. The number
40 of countries associated with impacts was best explained by the type of introduction pathway
41 (i.e., aquaculture or fisheries). We also discovered that alien species introduced through
42 aquaculture belonging to Cypriniformes and having a broad diet were the most widely
43 introduced and established species. The same was observed for species introduced through
44 ornamental pathways that were mainly native to tropical regions.

45 **Main conclusions**

46 Considering both intrinsic and extrinsic drivers is important when analyzing the invasion
47 success of freshwater fish and disentangling the different invasion steps. These findings have
48 strong implications for anticipating the profile of species with a high potential to invade a large
49 number of countries.

50

51 **Key words: aquaculture, ecology, exotic, freshwater fish, introduction pathways, invasion**
52 **steps, morphology, ornamental trade, socioeconomic, traits.**

53

54

55 **Introduction**

56 The rise of global trade has led to an increase in the introductions of invasive alien species
57 worldwide (Seebens et al., 2017). Nowadays, biological invasions are recognized as a major
58 threat to biodiversity, as they are the second cause of species extinction worldwide (Bellard et
59 al., 2016). Freshwater fish are among the most introduced taxa, and non-native freshwater fish
60 are now established in all biogeographical realms (Gozlan, 2008; Leprieur et al., 2008).
61 Established non-native freshwater fish species have diverse impacts, ranging from local
62 hybridization with native fauna – such as between the invasive rainbow trout (*Oncorhynchus*
63 *mykiss*) and native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in Canadian rivers
64 as reported by Muhlfeld et al., (2009) – to profound changes in species assemblages, leading to
65 taxonomic homogenization across large regions such as the Laurentian Great Lakes (Campbell
66 and Mandrak, 2020).

67 Nonetheless, not all introduced non-native fish species become established or have impacts.
68 Previous studies have shown that the success of each step of the invasion is influenced by three
69 categories of drivers: species characteristics, ecological characteristics of the native or recipient
70 ecosystems, and socioeconomic characteristics. Regarding species characteristics, non-native
71 fish species with a broad food spectrum are more establish more easily than more specialized
72 species (Ruesink, 2005). Likewise, for ecological characteristics, the size of the native range
73 influences the establishment and spread of non-native species (Marchetti et al., 2004a).
74 Concerning socioeconomic characteristics, some introduction pathways are known to be an
75 important source of freshwater fish introductions and establishments such as aquaculture and
76 ornamental trade (Gozlan et al., 2010). Socioeconomic characteristics can also relate to the
77 human use of fish, as the development of the ornamental trade has caused a recent rise in fish
78 introductions (Magalhães and Jacobi, 2013). Moreover, we can expect a strong interaction
79 between species characteristics and socioeconomic drivers. For instance, species introduced

80 through the aquaculture trade are more likely to be large species (Su et al., 2020), while those
81 introduced through ballast waters are more likely to be small species (Wonham et al., 2000).
82 Understanding the different characteristics that promote invasions is extremely important in
83 order to improve predictions about future invasions (Pyšek et al., 2020).

84 Several papers have focused on understanding the characteristics of successful invasive
85 freshwater fish species using quantitative analysis (e.g., García-Berthou, 2007; Snyder et al.,
86 2014; Su et al., 2020). However, species, ecological, and socioeconomic characteristics have
87 rarely been studied together at the global scale for freshwater fish (but see (Ruesink, 2005;
88 Pyšek et al., 2020). Indeed, most studies are conducted at a local scale with the analyses
89 performed on a limited number of species (Marchetti et al., 2004b; Ribeiro et al., 2008), often
90 without considering the different types of drivers (Ribeiro et al., 2008) or the steps of the
91 invasion process (e.g., García-Berthou, 2007, Ruesink, 2005; Lawson and Hill, 2021). As a
92 result, there is currently no consensus about the drivers influencing the invasion success of
93 freshwater fish globally (but see García-Berthou, 2007).

94 To fill this gap, we aimed to determine the drivers of the different steps of invasions (i.e.,
95 introduction, establishment, and impact) of freshwater fish species at the global scale using a
96 statistical modeling approach. For 307 freshwater fish species, we considered their species
97 (functional and morphological traits), ecological (features of the native ecosystems of the
98 species), and socioeconomic characteristics (introduction pathways and human use). We
99 investigated the link between these characteristics and the invasion patterns measured as the
100 number of countries where each species is introduced, established, and reported to impact the
101 native fauna or recipient ecosystem. We built our models based on initial assumptions for each
102 invasion step. First, we hypothesized that the species characteristics influencing the
103 introduction success are dependent on the introduction pathway (e.g., given that large-bodied
104 fishes are more interesting for anglers, they have a greater chance of being introduced through

105 the “angling” pathway; Peoples and Midway, 2018), which is itself influenced by the native
106 region of non-native species (e.g., species from the ornamental trade tend to be native in tropical
107 countries, Gertzen et al., 2008). As the establishment step depends on the adequacy between
108 the recipient ecosystem and the needs of the species, we hypothesize the higher success of
109 generalist species (i.e., broad diet) and species introduced in large numbers (i.e., with high
110 propagule pressure). High parental care has also been highlighted in several studies as an
111 important characteristic influencing establishment (Marchetti et al., 2004b; Lawson and Hill,
112 2021). Few studies have focused on the impact step. However, it has already been demonstrated
113 that species at the top trophic levels have a large impact, notably because prey in the new
114 environment are naive to the new predator (Moyle and Light, 1996; Howeth et al., 2016). We
115 can hypothesize that species with a nekton diet will have a greater impact than species at low
116 trophic levels.

117 **Material and methods**

118 **Species-level variables influencing the invasion success of freshwater fish**

119 To understand the drivers of success in exotic freshwater fish introduction, establishment, and
120 impact, we compiled species-level variables pertaining to their species, ecological, and
121 socioeconomic characteristics. We chose these variables because they are assumed to influence
122 species invasions (see Table 1 for justifications and hypotheses; Pyšek et al., 2020). We
123 obtained 20 species-level variables from five data sources: (i) FishBase (Froese and Pauly,
124 2019, version 19.04, accessed with the “rfishbase” R package; Boettiger et al., 2012), which
125 includes data on the invasive status, characteristics, and human use of 34,300 fish species at the
126 global scale; (ii) the FISHMORPH morphological database (Brosse et al., 2021), which
127 includes information on the morphological traits of 9,150 fish species; (iii) the database on
128 freshwater fish occurrences compiled by Tedesco et al. (2017), which has distribution data for

129 14,953 freshwater fish species in 3,119 basins worldwide; (iv) the global biogeographical
130 regions of freshwater fish (Leroy et al., 2019); and (v) the world climate database WorldClim
131 (Fick and Hijmans, 2017). We summarized all variables in Table 1 and describe them in detail
132 hereafter.

133 **Species characteristics**

134 We defined freshwater fish as all species with a freshwater habitat listed as one of their preferred
135 habitats in the table *species()* of the “rfishbase” R package.

136 *Main diet and number of diets* – To retrieve data on species diets, we used the “FoodI” column
137 of the *fooditems()* table of the “rfishbase” R package. We used two variables: (i) the most
138 represented diet for each species as the main diet and (ii) the total number of diets (Table 1). In
139 the rare cases (37 out of 307 species considered here) where several diets were equally
140 represented, we chose the most represented diet within the order. We made an exception for
141 *Megalops atlanticus* to which we had associated the “nekton” main diet, because this species,
142 which is a known predator of crabs and small fish (Planquette et al., 1996), has two main diets
143 that are also the two most represented diets of the order.

144 *Swimming ability* – To analyze the influence of swimming ability on invasion success, we used
145 two variables from Su et al. (2019). First, we used the pectoral fin vertical position (i.e., ratio
146 of pectoral fin position relative to body depth), which reflects the swimming style (Table 1).
147 Lateral pectoral fins are used for propulsion and fine movements, whereas ventral pectoral fins
148 often characterize fish with less precise movements (Blake, 2004; Su et al., 2019). Second, we
149 used the ratio of body length to body depth, which reflects fish hydrodynamics (Villéger et al.,
150 2017; Su et al., 2019) (Table 1).

151 *Parental care* – We used the parental care variable from the “RepGuild1” column of the
152 *species()* table of the “rfishbase” R package (Table 1).

153 *Total length (TL)* – To gather this information, we used the “TL” column of the
154 *morphometrics()* table of the “rfishbase” R package. As a species can have several different
155 total length, we took the median of all the given total length for each species.

156 *Species taxonomy* – We used FishBase as the taxonomic reference (Froese and Pauly, 2019).
157 For each species, we completed the order using the *load_taxa()* table from the “rfishbase” R
158 package. The number of species per order was heterogeneous, which can cause statistical issues
159 due to class imbalances, especially for minority classes (i.e., orders with only one or a few
160 species). Therefore, we kept the main orders (i.e., Characiformes, Cypriniformes,
161 Cyprinodontiformes, Perciformes, and Siluriformes) in the models and grouped together the
162 remaining orders in the “other” category.

163 **Ecological characteristics**

164 *Main native bioregion* – Freshwater fish have evolved in isolated biogeographical regions for
165 the past 10-20 million years (Leroy et al., 2019). Consequently, each bioregion has distinct
166 characteristics pertaining to its environmental conditions, faunistic composition, and associated
167 interactions. In addition, biogeographical regions broadly cover the main geopolitical regions
168 of the world, with distinct intra-region and inter-region properties in terms of species
169 displacement and propagule pressure. Hence, the region of origin of a species is a proxy of
170 several characteristics: environmental conditions, diversity of interactions during evolutionary
171 history, and chances of introduction to non-native ecosystems (Table 1). We defined two
172 variables based on the biogeographical regions of Leroy et al (2019): the number of native
173 bioregions (defined as bioregions where the species has native occurrences) and the main
174 bioregion, defined as the bioregion with the highest number of native basins where the species
175 is found. It is important to note that 85% of the species considered here have only one bioregion.
176 We excluded species that did not occur within the limits of the bioregions. A total of 2 species

177 equally occurred in two native bioregions. For these species, we selected one region at random
178 and verified whether this choice had an impact on the model results using sensitivity analysis.

179 *Temperature amplitude, minimum and maximum temperature in the native basins* – We used
180 the minimum temperature of the coldest month and the maximum temperature of the warmest
181 month from Worldclim (Fick and Hijmans, 2017) to derive two variables: annual maximum
182 temperature and temperature amplitude (Table 1). We excluded the annual minimum
183 temperature, as this variable was correlated to temperature amplitude. We only took into
184 account the 0.95 quantile of the maximum temperature of the warmest month and the 0.05
185 quantile of the minimum temperature of the coldest month across the native basins for each
186 species to avoid extreme outlier values.

187 **Socioeconomic drivers**

188 *Introduction pathways* – Using the *introduction()* table from the “rfishbase” R package, we
189 considered each pathway as an independent variable (Table 1). Therefore, species could have
190 several introduction pathways. We filtered out pathways containing only a few species. We thus
191 reclassified pathways documented in FishBase into the seven following categories: aquaculture,
192 sport/angling, species control, diffusion, accidental, fisheries, and ornamental trade
193 (Appendix 1).

194 *Use by humans* – Four columns of the *species()* table in the “rfishbase” R package indicate the
195 human use of species through fisheries (“Importance” column), bait (“Usedasbait” column),
196 sport (“GameFish” column), or aquariums (“Aquarium” column). If a species is used in at least
197 one of these four sectors (i.e., belonging to a category other than “never/rarely,” “of no interest,”
198 “of potential interest,” or “potential”), we considered this species to be used by humans.

199 *Table 1: Variable descriptions.*

Variable type	Variable	Variable modalities	Hypothesis / Justification
---------------	----------	---------------------	----------------------------

Response variable	Number of countries where the species: (i) is introduced (ii) is established (iii) has ecological impacts (for all species and the ornamental and aquaculture pathways)		
Species characteristics	Main diet	<ul style="list-style-type: none"> ▪ Detritus ▪ Nekton ▪ Plants ▪ Zoobenthos ▪ Zooplankton 	Broad food spectrum, piscivorous diet, as well as some specialized diets facilitate establishment (Ruesink, 2005; Tonella et al., 2018). A nekton diet can be associated with species having an impact (Moyle and Light, 1996; Howeth et al., 2016).
	Number of diets	Quantitative variable	
	Hydrodynamics	Quantitative variable	
	Pectoral fin vertical position	Quantitative variable	Good swimming ability enables fish to colonize new regions, spread, establish, and have wide impacts (Carvajal-Quintero et al., 2019).
	Parental care	Ordered categorical variable <ul style="list-style-type: none"> ▪ Non-guarder ▪ Guarder ▪ Bearer 	A high level of parental care facilitates establishment (Marchetti et al., 2004b; Lawson and Hill, 2021).
	Total length	Quantitative variable	At the introduction step, the body length of successful species is linked to the introduction pathway (Wonham et al., 2000; Su et al., 2020). At the establishment step, body length depends on the environmental conditions (Vila-Gispert et al., 2005). At the impact step, small species can have greater impacts (Marchetti et al., 2004).
	Taxonomy	<ul style="list-style-type: none"> ▪ Cypriniformes ▪ Cyprinodontiformes ▪ Siluriformes ▪ Characiformes ▪ Other 	Order is a surrogate for missing characteristics that could influence species success at different stages of the invasion.
Ecological characteristics	Temperature amplitude in the native basins	Quantitative variable	Temperature amplitude in native basins can be a proxy of temperature tolerance.
	Maximum temperature in the native basins	Quantitative variable	Temperature tolerance influences the establishment and spread of invasive species (Kolar and Lodge, 2002; Marchetti et al., 2004b; Snyder et al., 2014).
	Main native bioregion	<ul style="list-style-type: none"> ▪ Nearctic ▪ Palearctic ▪ Sino-Oriental ▪ Neotropical ▪ Ethiopian ▪ Madagascan 	Native bioregions reflect socioeconomic characteristics, propagule pressure, and environmental conditions.

Socioeconomic characteristics	Aquaculture	1/0 Quantitative variable	Introduction pathways constrain the characteristics of introduced species (Wonham et al., 2000; Su et al., 2020). The number of introduction pathways is linked to high propagule pressure.
	Sport/Angling		
	Accidental		
	Ornamental		
	Fisheries		
	Diffusion		
	Species control		
	Number of introduction pathways		
	Use by humans	Yes/No	Species used by humans have greater chances of being introduced than those not used by humans.

200

201 **Response variables**

202 In this study, we considered three steps of the invasion: introduction, establishment, and impact.

203 We gathered data on three variables that reflect these three steps: the number of countries where
 204 species are introduced, the number of countries where introduced species are established, and
 205 finally, the number of countries where the established species have impacts. To obtain
 206 information about these variables for each species, we used the *introductions()* function of the
 207 “rfishbase” R package. This table describes the introduction events of fish species, giving the
 208 location of the introduction, the species concerned, as well as the establishment and impact
 209 status of the species.

210 *Number of countries where species are introduced, established, and have impacts*

211 We used the locations found in the “TO” column of the *introduction()* table of the “rfishbase”
 212 R package. It should be noted that some species were simply transported to the new location
 213 without being introduced to the wild. These species were impossible to separate from others,
 214 although they remain scarce because most alive imported species are introduced (intentionally
 215 or accidentally) to the natural environment (Ju et al., 2020; Magalhães et al., 2020). Thus, we
 216 assumed that all species were introduced to the wild. The locations listed in FishBase were not

217 standardized at a specific spatial scale (names ranged from the names of cities to entire
218 continents), so we manually harmonized names to the country scale. We excluded all records
219 above the country scale. We grouped islands located far from their country by archipelago or
220 considered them separately when they did not belong to an archipelago. As some of the
221 introductions were old, the listed countries no longer exist and could not be grouped or
222 assimilated with the new country. This was the case for the USSR and Korea. We therefore
223 considered these countries independently. When the spatial grain was the river or lake, we
224 considered all the riparian countries independently. We listed as “Unknown” any locations
225 given at a larger scale than a country (e.g., “Europe”) or locations that could not be identified.
226 The list of 208 countries considered in this study is available in Appendix 2.

227 For each species, we counted the number of countries where the species were introduced,
228 established, or had impacts. Concerning the establishment step, all the species noted as “Yes,”
229 “Probably Yes,” “Established,” or “Probably established” in the “Estabwild” column of the
230 *introduction()* table were taken as species established in the wild in the considered locations.
231 We removed from the analysis the species that were listed as established but not introduced
232 beforehand, as we could not access the establishment location of these so-called non-introduced
233 species. We took as established any species that had an impact but were not established (i.e.,
234 “No” or “Probably no” in the “Estabwild” column) or had an unknown establishment status.
235 Concerning the impact step, we considered that all the species noted as “Yes,” “Probably
236 some,” or “Some” in the “EcolEff” column of the *introduction()* table had ecological impacts
237 in the considered locations.

238 We obtained 840 species with an introduced status (307 introduced species, 533 non-introduced
239 species). For the 307 introduced species, the number of countries where the species were
240 introduced was provided. Among these 307 introduced species, 217 species were established
241 in at least one country and 117 had ecological impacts in at least one country.

242 **Statistical analysis**

243 To determine the characteristics of the species at each step of the invasion process, we used
244 generalized linear models (GLM) to analyze the influence of species, ecological, and
245 socioeconomic characteristics on the number of countries where the species are introduced,
246 established, or have impacts. First, we assessed the correlations between all the 20 explanatory
247 variables. We used the *ggcorr()* R function of the GGally package (Schloerke et al., 2020) to
248 explore the Spearman correlations between quantitative variables. We also used the
249 *model.matrix()* from the stats package (R Core Team, 2020) to separate each modality of the
250 numerical variables into binary variables. We then used the *cor()* function (stats package; R
251 Core Team, 2020) to explore the Pearson correlations between the new binary variables and
252 between the binary and quantitative variables. To avoid multicollinearity, we centered the
253 variables “total length,” “temperature amplitude in the native region,” and “number of diets.”
254 We performed GLMs considering all the species, regardless of their introduction pathway, to
255 explain the number of countries where the species (i) were introduced, (ii) were established,
256 and (iii) had impacts (Appendix 3). We used the 20 explanatory variables and six interactions
257 between the variables: the interactions between total length and temperature amplitude,
258 between total length and order, between total length and ornamental pathway, between total
259 length and sport/angling pathway, between total length and aquaculture pathway, and between
260 number of diets and order (Appendix 3). We also conducted the same analyses while
261 considering only the species introduced through the aquaculture pathway or through the
262 ornamental trade pathway (i.e., 11 variables and 3 interactions; see Appendix 3).

263 As our data were count data, we computed these GLMs with Poisson distributions or negative
264 binomial distributions when our response variables were overdispersed. To check for
265 overdispersion, we used the *dispersiontest()* function from the “AER” R package (Kleiber and
266 Zeileis, 2008). Then we used the *stepAIC()* function from the “MASS” R package (Venables

267 and Ripley, 2002) and a stepwise selection to choose the best model based on the Akaike
268 information criterion. For each model, a pseudo-r² was estimated using the following formula:
269 $1 - \text{Model Deviance} / \text{Model Null Deviance}$. We identified the significant variables of each
270 model using the Anova() function from the “car” R package (Fox and Weisberg, 2019). The
271 variable importance of each variable in the models (i.e., absolute value of the t-statistic of each
272 model variable) was calculated using the varImp() function from the “caret” R package (Kuhn,
273 2008).

274 To take into account the potential fluctuations due to the randomly chosen main diet and main
275 regions for some species, we performed sensitivity analysis. For the species with several main
276 diets or several main native regions, we randomly selected the main diet and the main native
277 region. Then we performed the above GLMs on the new dataset. We repeated the process 100
278 times to observe the variation in the results due to the random choices. The results of these
279 analyses are presented in Appendix 4.

280 **Results**

281 **All species**

282 Considering the 307 introduced species, species introduced in a high number of countries were
283 associated with a high number of different introduction pathways (variable importance [VI] =
284 10), a high level of parental care (VI = 5.3 for the linear relation), had aquaculture (VI = 4.5)
285 or fisheries (VI = 2.7) as one of their introduction pathways, and had a high number of diets
286 (VI = 2.4) (Fig. 1a., Fig. 4). Siluriformes with a high number of diets also tend to be introduced
287 in many countries (VI = 2.3). The establishment step model showed similar results to the
288 introduction model for selected variables (Fig.1b., Fig. 4), except that the species established
289 in a high number of countries were not significantly more introduced through the aquaculture
290 pathway. Finally, species with impacts in a high number of countries were associated with most

291 of the pathways (except for species control, accidental, and aquaculture), a high level of parental
292 care, and a high number of diets when species were from the Siluriformes order (Fig. 1c., Fig.
293 4). Nonetheless, parental care was only significant in 22% of models in sensitivity analysis,
294 thus reducing its robustness (Appendix 4C).

295

296 **Species introduced through the aquaculture pathway**

297 Species introduced through aquaculture (Fig. 2a.) in a high number of countries were associated
298 with a high number of diets (VI = 2.9) and more often belonged to the Cypriniformes order (VI
299 = 1.6). They were also more often associated with high parental care (significant variable in
300 57% of models in sensitivity analysis) (Fig. 2a., Appendix 4A). In terms of establishment,
301 species established in many countries by aquaculture had a high number of diets (VI = 3.8) and
302 belonged to all orders except for Characiformes, even though this tendency was less robust for
303 the Cyprinodontiformes order (Appendix 4). They were also often associated with high parental
304 care (significant variable in 76% of models; Fig. 3b., Appendix 4B).

305

306 **Species introduced through the ornamental trade pathway**

307 We analyzed the characteristics of 126 species introduced through ornamental trade (Fig. 3a.).
308 Species introduced to many countries were not hydrodynamic (VI = 5.5), were native to the
309 Neotropical (VI = 2.5) or Sino-Oriental regions (VI = 2.3), and had a high number of diets (VI
310 = 1.6).

311 Concerning the establishment step (Fig. 3b.), we considered a subset of 70 established species
312 among those introduced through the ornamental trade pathway. Species established in many
313 countries were not hydrodynamic (VI = 4.9), were from the Cyprinodontiformes (VI = 4.3) or

314 Cypriniformes (VI = 2.4) orders, and mainly came from the Ethiopian (VI = 1.2) or Neotropical
315 (VI = 1.1) regions.

316 **Discussion**

317 Using the socioeconomic, ecological, and species characteristics of 307 freshwater fish species,
318 we were able to identify a profile of successful invasions for each step of the invasion process
319 (Figure 4, Appendix 5). As we hypothesized, we found that species characterized by a broad
320 diet and high parental care as well as multiple socioeconomic pathways of introductions,
321 including fisheries and aquaculture, were particularly successful at being introduced and
322 established in multiple countries. By contrast, socioeconomic characteristics seem highly
323 important to explain the impact of freshwater fish in many countries, and contrary to our
324 hypothesis, diet did not have a significant effect on the success of this step.

325 **Introduction step**

326 We found that species introduced to many countries have specific characteristics. As
327 hypothesized, multiple introduction pathways favored widespread introductions, with different
328 entry routes increasing the chances of being transported and introduced in many locations. For
329 example, the common carp is introduced through six of the seven pathways considered here,
330 but some of the pathways are specific to certain countries. This is the case with the common
331 carp introduced to several countries via aquaculture (e.g., Australia, Shearer and Mulley, 1978;
332 Varadi and Gorda, 2021), to New Zealand and South Africa for ornamental purposes (De Moor
333 and Bruton, 1988; Hanchet, 1990, Froese and Pauly, 2019; Varadi and Gorda, 2021), and to
334 Finland for angling (Froese and Pauly, 2019). Species introduced to a high number of countries
335 also tend to have a high level of parental care and a high number of diets: for example,
336 *Oreochromis mossambicus* and *Oreochromis niloticus*, respectively introduced to 97 and 94
337 countries, are bearers and have at least four diets (Froese and Pauly, 2019). This result confirms

338 our initial hypothesis, as these two characteristics have already been highlighted in previous
339 studies, although only at the state or country scale and for the establishment step (Marchetti et
340 al., 2004a in California; Tonella et al., 2018 in Brazil; Chan et al., 2021 in Singapore; Lawson
341 and Hill, 2021 in Peninsular Florida). Nonetheless, the role played by parental care in the
342 introduction step of the invasion process has not yet been reported, and the underlying
343 mechanisms remain to be clarified (e.g., Marchetti et al., 2004a). One possible explanation
344 could be that species with high parental care tend to be more introduced, because their
345 reproduction is easier in captivity. For instance, several species of Poecilids (e.g., guppies,
346 *Poecilia reticulata*) and Cichlids (e.g. *Haplochromis* sp. or *Cichlasoma* sp.) are popular
347 aquarium fish known to be highly prolific and easy to rear (Bianchi, 1993).

348 **Establishment**

349 For species established in many countries, we found characteristics similar to the introduction
350 step: high number of pathways, high parental care, and high number of diets. The high number
351 of introduction pathways is linked to the high propagule pressure, which is known to be one of
352 the main characteristics of invasion success (Jeschke and Strayer, 2006). High parental care
353 maximizes offspring survival in the presence of competitors, thus providing an advantage that
354 can favor establishment (Levine and D'Antonio, 1999). Moreover, generalist diets allow
355 introduced species to adapt in different environments and thus provide the opportunity to
356 establish in a wide range of environments (Tonella et al., 2018).

357 Despite this common overall pattern of introduction and establishment characteristics, we found
358 several noteworthy differences. For example, although species introduced through the
359 aquaculture pathway are introduced in many countries, their establishment success remains
360 limited. This result is counterintuitive, as aquaculture is recognized as the most important
361 introduction pathway of non-native freshwater fish (Gozlan et al., 2010). Our results suggest

362 that even though aquaculture allows the establishment of many different species, it does not
363 result in these species establishing in many different countries. This trend can be explained by
364 the concentration of aquaculture production in Asia, especially in China, which produces a
365 higher diversity of species (Metian et al., 2020). The way in which the species are cultured in
366 each country also affects the probabilities of establishment. For example, species reared in and
367 escaping from natural ponds are more likely to establish, because the individuals often escape
368 in high numbers (Gu et al., 2022). This trend could also reflect the efficiency of management
369 methods set by governments to limit or avoid fish escapes (Kolar et al., 2010). We can also
370 hypothesize that some species introduced through aquaculture are not able to survive and
371 reproduce in natural environments (e.g., East Asian carp in North Europe; Lehtonen, 2002).

372 **Ecological impact**

373 The variables influencing the number of countries where species have ecological impacts are
374 distinct from those influencing the introduction and establishment steps. Contrary to our
375 hypothesis, diet did not have a significant impact on the impact step. Fisheries, ornamental
376 trade, and angling along with the diffusion of already established species were the major
377 pathways favouring non-native species impacts. Surprisingly, the aquaculture pathway did not
378 stand out as an important variable despite the substantial impact of some cultured fish. In fact,
379 the impacts of fish introduced through aquaculture may be understudied due to their economic
380 benefits (Gozlan, 2008; Haubrock et al., 2022), which explains why aquaculture does not stand
381 out as an important variable. For example, the channel catfish (*Ictalurus punctatus*) is known
382 to be responsible for the decline of native species outside its native range (Townsend and
383 Winterbourn, 1992). Though widely introduced in Brazil for aquaculture, no ecological impact
384 has been recorded in FishBase for the species in this country (Vitule et al., 2009; Froese and
385 Pauly, 2019). At the global scale, data on freshwater fish impacts are incomplete, which hinders
386 the identification of important characteristics for this invasion step (Vitule et al., 2009).

387 Introduction pathways are not the only important variables for the impact step. Indeed,
388 Siluriformes are introduced, established, and have impacts in many countries, but only if they
389 have a broad diet. This tendency seems to be driven by a few species that have a broad diet and
390 are present in a high number of countries (i.e., *Clarias angilaris*, *Ictalurus punctatus*, *Ameiurus*
391 *melas*, *Ameiurus nebulosus*, *Silurus glanis*).

392 **Importance of interactions between pathways and species characteristics**

393 In this study, we highlighted differences in the species characteristics according to the
394 introduction pathways. Preliminary analysis comparing introduced and non-introduced species
395 highlighted the influence of introduction pathways on invasion success (Appendix 6).
396 Considering all the species, the overrepresentation of species native to the Palearctic and Sino-
397 Oriental regions among the introduced species could be due to the influence of the two most
398 important pathways: aquaculture and ornamental trade. Indeed, these regions are economically
399 well developed, making them more prone to export fish species for the aquaculture (FAO,
400 2012). This may also be linked to the early development of aquaculture in these regions, in
401 particular in the Palearctic region (Balon, 1995). With the development of aquaculture in
402 tropical countries (Garlock et al., 2020), this trend is likely to spread throughout developing
403 regions of the globe. Considering the models per pathway, the species introduced and
404 established in many countries through aquaculture are similar to those of the global pool (i.e.,
405 high number of diets, high parental care). They also tend to be from the Cypriniformes order.
406 This can be explained by human selection. Fish from the Cypriniformes order such as carp have
407 been cultured for centuries (Balon, 2004) and thus constitute the main species produced in
408 global aquaculture (FAO, 2020).

409 However, species introduced and established in many countries through the ornamental trade
410 are not hydrodynamic and are more often native to the Neotropical and Sino-Oriental regions.

411 These characteristics correspond to the description of the most popular aquarium fish such as
412 *Poeciliids* and *tetras* (Duggan et al., 2006; Gertzen et al., 2008), thus pointing to the strong
413 influence of propagule pressure.

414 **Limitations and recommendations for future studies**

415 It is important to note that the similarity between the introduction and establishment steps can
416 be partially explained by a detection bias: introductions that fail to establish have less chance
417 of being reported than successful introductions (Drake, 2007). Nonetheless, a non-negligible
418 number of failed introductions were reported here (90 out of 307). We used the number of
419 countries where species are introduced, established, and have impacts as an indicator of alien
420 success, although the size of the countries is highly variable, which implies possible biases.
421 Species established in many small countries are considered to be more established than species
422 established in a limited number of large countries, even though they may both cover the same
423 area. This bias could be corrected by using the number of basins, but we only have this
424 information for the establishment step (Tedesco et al., 2017). Nonetheless, the number of
425 countries where species have become established is significantly and positively correlated to
426 the number of basins, thus minimizing the importance of the bias (Appendix 8). Moreover,
427 some of our results can vary at the local scale, because the characteristics of the recipient
428 environment can significantly influence the outcome of an introduction (Vila-Gispert et al.,
429 2005). To improve future studies, more data should to be collected in relation to the impact step
430 as well as certain characteristics such as fecundity, which has been shown to influence the
431 establishment of species at the local scale (Vila-Gispert et al., 2005).

432 **Conclusion**

433 This study provides a comprehensive understanding of the characteristics that allow for the
434 success of the whole invasion process. It highlights the importance of considering different

435 invasion steps separately to account for the wide variety of extrinsic and intrinsic factors
436 involved in invasion models and disentangle the effects of introduction pathways. These results
437 can be useful in order to improve screening tools. For example, the invasiveness tool of
438 FishBase only takes into account the introduction pathway and the climate adequacy between
439 the native and recipient environment to determine the potential invasiveness of a species
440 (Froese and Pauly, 2019). By contrast, our results stress the importance of considering a wider
441 variety of characteristics. The findings also show the importance of determining not only the
442 invasive status of a species but also the profile of species with the potential to invade large
443 areas. Ultimately, this approach considering the different steps and pathways of invasion could
444 be helpful to better identify the determinants of invasion success in other taxa (Capellini et al.,
445 2015).

446

447 **Data availability statement:**

448 All the R code necessary to generate the data and the results present in the paper will be available on
449 GitHub after the acceptance of the paper. Used data also include open access data : (i) FishBase
450 (Froese and Pauly, 2019, version 19.04, accessed with the “rfishbase” R package; Boettiger et al.,
451 2012); (ii) the FISHMORPH morphological database (Brosse et al., 2021); (iii) the database on
452 freshwater fish occurrences compiled by Tedesco et al. (2017); (iv) the global biogeographical regions
453 of freshwater fish (Leroy et al., 2019); and (v) the world climate database WorldClim (Fick and
454 Hijmans, 2017).

455 **References**

- 456 Balon, E. K. (1995). Origin and domestication of the wild carp, *Cyprinus carpio* : From
457 Roman gourmets to the swimming flowers. *Aquaculture*, 129(1), 3-48. <https://doi.org/10.1016/0044->
458 8486(94)00227-F
- 459 Balon, E. K. (2004). About the oldest domesticates among fishes. *Journal of Fish Biology*, 65,
460 1-27. <https://doi.org/10.1111/j.0022-1112.2004.00563.x>
- 461 Bellard, C., Genovesi, P., & Jeschke, J. M. (2016). Global patterns in threats to vertebrates by
462 biological invasions. *Proceedings of the Royal Society B: Biological Sciences*, 283(1823), 20152454.
463 <https://doi.org/10.1098/rspb.2015.2454>
- 464 Bianchi, I. (1993). *L'aquarium tropical d'eau douce* (De Vecchi).
- 465 Blake, R. W. (2004). Fish functional design and swimming performance. *Journal of Fish*
466 *Biology*, 65(5), 1193-1222. <https://doi.org/10.1111/j.0022-1112.2004.00568.x>
- 467 Brosse, S., Charpin, N., Su, G., Toussaint, A., Herrera-R, G. A., Tedesco, P. A., & Villéger, S.
468 (2021). FISHMORPH : A global database on morphological traits of freshwater fishes. *Global*
469 *Ecology and Biogeography*, 30(12), 2330-2336. <https://doi.org/10.1111/geb.13395>
- 470 Campbell, S. E., & Mandrak, N. E. (2020). Functional differentiation accompanies taxonomic
471 homogenization in freshwater fish communities. *Ecology*, 101(12), e03188.
472 <https://doi.org/10.1002/ecy.3188>
- 473 Capellini, I., Baker, J., Allen, W. L., Street, S. E., & Venditti, C. (2015). The role of life
474 history traits in mammalian invasion success. *Ecology Letters*, 18(10), 1099-1107.
475 <https://doi.org/10.1111/ele.12493>
- 476 Carvajal-Quintero, J., Villalobos, F., Oberdorff, T., Grenouillet, G., Brosse, S., Hugueny, B.,
477 Jézéquel, C., & Tedesco, P. A. (2019). Drainage network position and historical connectivity explain
478 global patterns in freshwater fishes' range size. *Proceedings of the National Academy of Sciences of*
479 *the United States of America*, 116(27), 13434-13439. <https://doi.org/10.1073/pnas.1902484116>

480 Chan, J., Zeng, Y., & Yeo, D. C. J. (2021). Invasive species trait-based risk assessment for
481 non-native freshwater fishes in a tropical city basin in Southeast Asia. *PLOS ONE*, *16*(3), e0248480.
482 <https://doi.org/10.1371/journal.pone.0248480>

483 De Moor, I. J., & Bruton, M. N. (1988). *Atlas of alien and translocated indigenous aquatic*
484 *animals in southern Africa* [Report]. National Scientific Programmes Unit: CSIR.
485 <https://researchspace.csir.co.za/dspace/handle/10204/2416>

486 Drake, J. M. (2007). Parental investment and fecundity, but not brain size, are associated with
487 establishment success in introduced fishes. *Functional Ecology*, *21*(5), 963-968.
488 <https://doi.org/10.1111/j.1365-2435.2007.01318.x>

489 Duggan, I. C., Rixon, C. A. M., & MacIsaac, H. J. (2006). Popularity and Propagule Pressure :
490 Determinants of Introduction and Establishment of Aquarium Fish. *Biological Invasions*, *8*(2),
491 377-382. <https://doi.org/10.1007/s10530-004-2310-2>

492 FAO. 2012. *The State of World Fisheries and Aquaculture 2012*. Rome. 209 pp.

493 FAO. (2020). *The State of World Fisheries and Aquaculture 2020*. FAO.
494 <https://doi.org/10.4060/ca9229en>

495 Fick, S., & Hijmans, R. (2017). WorldClim 2 : New 1-km spatial resolution climate surfaces
496 for global land areas. *International Journal of Climatology*, *37*. <https://doi.org/10.1002/joc.5086>

497 Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage,
498 Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

499 García-Berthou, E. (2007). The characteristics of invasive fishes : What has been learned so
500 far? *Journal of Fish Biology*, *71*, 33-55. <https://doi.org/10.1111/j.1095-8649.2007.01668.x>

501 Garlock, T., Asche, F., Anderson, J., Bjørndal, T., Kumar, G., Lorenzen, K., Ropicki, A.,...,
502 Tveterås, R. (2020). A Global Blue Revolution : Aquaculture Growth Across Regions, Species, and
503 Countries. *Reviews in Fisheries Science & Aquaculture*, *28*(1), 107-116.
504 <https://doi.org/10.1080/23308249.2019.1678111>

505 Gertzen, E., Familiar, O., & Leung, B. (2008). Quantifying invasion pathways : Fish
506 introductions from the aquarium trade. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(7),
507 1265-1273. <https://doi.org/10.1139/F08-056>

508 Gozlan, R. E. (2008). Introduction of non-native freshwater fish : Is it all bad? *Fish and*
509 *Fisheries*, 9(1), 106-115. <https://doi.org/10.1111/j.1467-2979.2007.00267.x>

510 Gozlan, R. E., Britton, J. R., Cowx, I., & Copp, G. H. (2010). Current knowledge on non-
511 native freshwater fish introductions. *Journal of Fish Biology*, 76(4), 751-786.
512 <https://doi.org/10.1111/j.1095-8649.2010.02566.x>

513 Gu, D. E., Wang, J. W., Xu, M., Mu, X. D., Wei, H., Yu, F. D., Fang, M.,... , Hu, Y. C.
514 (2022). Does aquaculture aggravate exotic fish invasions in the rivers of southern China? *Aquaculture*,
515 547, 737492. <https://doi.org/10.1016/j.aquaculture.2021.737492>

516 Hanchet, S. M. (1990). *The Effects of Koi Carp on New Zealand's Aquatic Ecosystems*.
517 Unknown Publisher.

518 Haubrock, P. J., Bernery, C., Cuthbert, R. N., Liu, C., Kourantidou, M., Leroy, B., Turbelin,
519 A.,..., Gozlan, R. E. (2022). Knowledge gaps in economic costs of invasive alien fish worldwide.
520 *Science of The Total Environment*, 803, 149875. <https://doi.org/10.1016/j.scitotenv.2021.149875>

521 Howeth, J. G., Gantz, C. A., Angermeier, P. L., Frimpong, E. A., Hoff, M. H., Keller, R. P.,
522 Mandrak,...., Lodge, D. M. (2016). Predicting invasiveness of species in trade : Climate match,
523 trophic guild and fecundity influence establishment and impact of non-native freshwater fishes.
524 *Diversity and Distributions*, 22(2), 148-160. <https://doi.org/10.1111/ddi.12391>

525 Jeschke, J. M., & Strayer, D. L. (2006). Determinants of vertebrate invasion success in Europe
526 and North America. *Global Change Biology*, 12(9), 1608-1619. <https://doi.org/10.1111/j.1365->
527 2486.2006.01213.x

528 Ju, R.-T., Li, X., Jiang, J.-J., Wu, J., Liu, J., Strong, D. R., & Li, B. (2020). Emerging risks of
529 non-native species escapes from aquaculture : Call for policy improvements in China and other

530 developing countries. *Journal of Applied Ecology*, 57(1), 85-90. <https://doi.org/10.1111/1365->
531 2664.13521

532 Kolar, C., Courtenay, W., & Nico, L. (2010). *Managing undesired or invading species*. Inland
533 fisheries management in North America, 3rd edition. American Fisheries Society, Bethesda,
534 Maryland, pp. 213-259.

535 Kolar, C. S., & Lodge, D. M. (2002). Ecological Predictions and Risk Assessment for Alien
536 Fishes in North America. *Science*, 298(5596), 1233-1236. <https://doi.org/10.1126/science.1075753>

537 Kuhn, M. (2008). Building Predictive Models in R Using the caret Package. *Journal of*
538 *Statistical Software*, 28(5), 1 - 26. doi:<http://dx.doi.org/10.18637/jss.v028.i05>

539 Lawson, K. M., & Hill, J. E. (2021). Life history strategies differentiate established from
540 failed non-native freshwater fish in peninsular Florida. *Diversity and Distributions*, 28(1), 160-172.
541 <https://doi.org/10.1111/ddi.13448>

542 Lehtonen, H. (2002). Alien Freshwater Fishes of Europe. In E. Leppäkoski, S. Gollasch, & S.
543 Olenin (Éds.), *Invasive Aquatic Species of Europe. Distribution, Impacts and Management*. Springer
544 Netherlands. pp. 153-161. https://doi.org/10.1007/978-94-015-9956-6_17

545 Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T., & Brosse, S. (2008). Fish Invasions
546 in the World's River Systems : When Natural Processes Are Blurred by Human Activities. *PLoS*
547 *Biology*, 6(2), e28. <https://doi.org/10.1371/journal.pbio.0060028>

548 Leroy, B., Dias, M. S., Giraud, E., Hugueny, B., Jézéquel, C., Leprieur, F., Oberdorff, T., &
549 Tedesco, P. A. (2019). Global biogeographical regions of freshwater fish species. *Journal of*
550 *Biogeography*, 46(11), 2407-2419. <https://doi.org/10.1111/jbi.13674>

551 Levine, J. M., & D'Antonio, C. M. (1999). Elton Revisited : A Review of Evidence Linking
552 Diversity and Invasibility. *Oikos*, 87(1), 15-26. <https://doi.org/10.2307/3546992>

553 Magalhães, A. L. B., Daga, V. S., Bezerra, L. A. V., Vitule, J. R. S., Jacobi, C. M., & Silva, L.
554 G. M. (2020). All the colors of the world : Biotic homogenization-differentiation dynamics of

555 freshwater fish communities on demand of the Brazilian aquarium trade. *Hydrobiologia*, 847(18),
556 3897-3915. <https://doi.org/10.1007/s10750-020-04307-w>

557 Magalhães, A. L. B. de, & Jacobi, C. M. (2013). Invasion risks posed by ornamental
558 freshwater fish trade to southeastern Brazilian rivers. *Neotropical Ichthyology*, 11, 433-441.
559 <https://doi.org/10.1590/S1679-62252013005000003>

560 Marchetti, M. P., Moyle, P. B., & Levine, R. (2004a). Alien fishes in California watersheds :
561 Characteristics of successful and failed invaders. *Ecological Applications*, 14(2), 587-596.
562 <https://doi.org/10.1890/02-5301>

563 Marchetti, M. P., Moyle, P. B., & Levine, R. (2004b). Invasive species profiling? Exploring
564 the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology*, 49(5),
565 646-661. <https://doi.org/10.1111/j.1365-2427.2004.01202.x>

566 Metian, M., Troell, M., Christensen, V., Steenbeek, J., & Pouil, S. (2020). Mapping diversity
567 of species in global aquaculture. *Reviews in Aquaculture*, 12(2), 1090-1100.
568 <https://doi.org/10.1111/raq.12374>

569 Moyle, P. B., & Light, T. (1996). Biological invasions of fresh water : Empirical rules and
570 assembly theory. *Biological Conservation*, 78(1-2), 149-161. [https://doi.org/10.1016/0006-](https://doi.org/10.1016/0006-3207(96)00024-9)
571 [3207\(96\)00024-9](https://doi.org/10.1016/0006-3207(96)00024-9)

572 Muhlfeld, C. C., Kalinowski, S. T., McMahon, T. E., Taper, M. L., Painter, S., Leary, R. F., &
573 Allendorf, F. W. (2009). Hybridization rapidly reduces fitness of a native trout in the wild. *Biology*
574 *Letters*, 5(3), 328-331. <https://doi.org/10.1098/rsbl.2009.0033>

575 Peoples, B. K., & Midway, S. R. (2018). Fishing pressure and species traits affect stream fish
576 invasions both directly and indirectly. *Diversity and Distributions*, 24(8), 1158-1168.
577 <https://doi.org/10.1111/ddi.12747>

578 Planquette, P., Keith, P., & Le Bail, P.-Y. (1996). *Atlas des poissons d'eau douce de*
579 *Guyane—Scientific Publications of the Muséum national d'Histoire naturelle, Paris* (Vol. 22).
580 Muséum National d'Histoire Naturelle, Ministère de l'Environnement, Paris.

581 <https://sciencepress.mnhn.fr/en/collections/patrimoines-naturels/atlas-des-poissons-d-eau-douce-de->
582 [guyane](https://sciencepress.mnhn.fr/en/collections/patrimoines-naturels/atlas-des-poissons-d-eau-douce-de-guyane)

583 Pyšek, P., Bacher, S., Kühn, I., Novoa, A., Catford, J. A., Hulme, P. E., Pergl, J., ...,
584 Blackburn, T. M. (2020). MAcroecological Framework for Invasive Aliens (MAFIA) : Disentangling
585 large-scale context dependence in biological invasions. *NeoBiota*, 62, 407-461.
586 <https://doi.org/10.3897/neobiota.62.52787>

587 Ribeiro, F., Elvira, B., Collares-Pereira, M. J., & Moyle, P. B. (2008). Life-history traits of
588 non-native fishes in Iberian watersheds across several invasion stages : A first approach. *Biological*
589 *Invasions*, 10(1), 89-102. <https://doi.org/10.1007/s10530-007-9112-2>

590 Ruesink, J. L. (2005). Global Analysis of Factors Affecting the Outcome of Freshwater Fish
591 Introductions : Outcome of Fish Introductions. *Conservation Biology*, 19(6), 1883-1893.
592 <https://doi.org/10.1111/j.1523-1739.2005.00267.x-i1>

593 Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., Elberg A., &
594 Crowley, J., (2020). GGally: Extension to 'ggplot2'. R package version 2.0.0. [https://CRAN.R-](https://CRAN.R-project.org/package=GGally)
595 [project.org/package=GGally](https://CRAN.R-project.org/package=GGally)

596 Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad,
597 S., ..., Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature*
598 *Communications*, 8(1), 14435. <https://doi.org/10.1038/ncomms14435>

599 Snyder, R. J., Burlakova, L. E., Karatayev, A. Y., & MacNeill, D. B. (2014). Updated invasion
600 risk assessment for Ponto-Caspian fishes to the Great Lakes. *Journal of Great Lakes Research*, 40(2),
601 360-369. <https://doi.org/10.1016/j.jglr.2014.03.009>

602 Su, G., Villéger, S., & Brosse, S. (2019). Morphological diversity of freshwater fishes differs
603 between realms, but morphologically extreme species are widespread. *Global Ecology and*
604 *Biogeography*, 28(2), 211-221. <https://doi.org/10.1111/geb.12843>

605 Su, G., Villéger, S., & Brosse, S. (2020). Morphological sorting of introduced freshwater fish
606 species within and between donor realms. *Global Ecology and Biogeography*, 29(5), 803-813.
607 <https://doi.org/10.1111/geb.13054>

608 Tedesco, P. A., Beauchard, O., Bigorne, R., Blanchet, S., Buisson, L., Conti, L., Cornu, J.-F.,
609 ..., Oberdorff, T. (2017). A global database on freshwater fish species occurrence in drainage basins.
610 *Scientific Data*, 4(1), 170141. <https://doi.org/10.1038/sdata.2017.141>

611 Tonella, L. H., Fugi, R., Vitorino, O. B., Suzuki, H. I., Gomes, L. C., & Agostinho, A. A.
612 (2018). Importance of feeding strategies on the long-term success of fish invasions. *Hydrobiologia*,
613 817(1), 239-252. <https://doi.org/10.1007/s10750-017-3404-z>

614 Townsend, C. R., & Winterbourn, M. J. (1992). Assessment of the Environmental Risk Posed
615 by an Exotic Fish : The Proposed Introduction of Channel Catfish (*Ictalurus punctatus*) to New
616 Zealand. *Conservation Biology*, 6(2), 273-282. <https://doi.org/10.1046/j.1523-1739.1992.620273.x>

617 Venables WN & Ripley BD (2002). *Modern Applied Statistics with S*, Fourth edition.
618 Springer, New York. ISBN 0-387-95457-0, <https://www.stats.ox.ac.uk/pub/MASS4/>

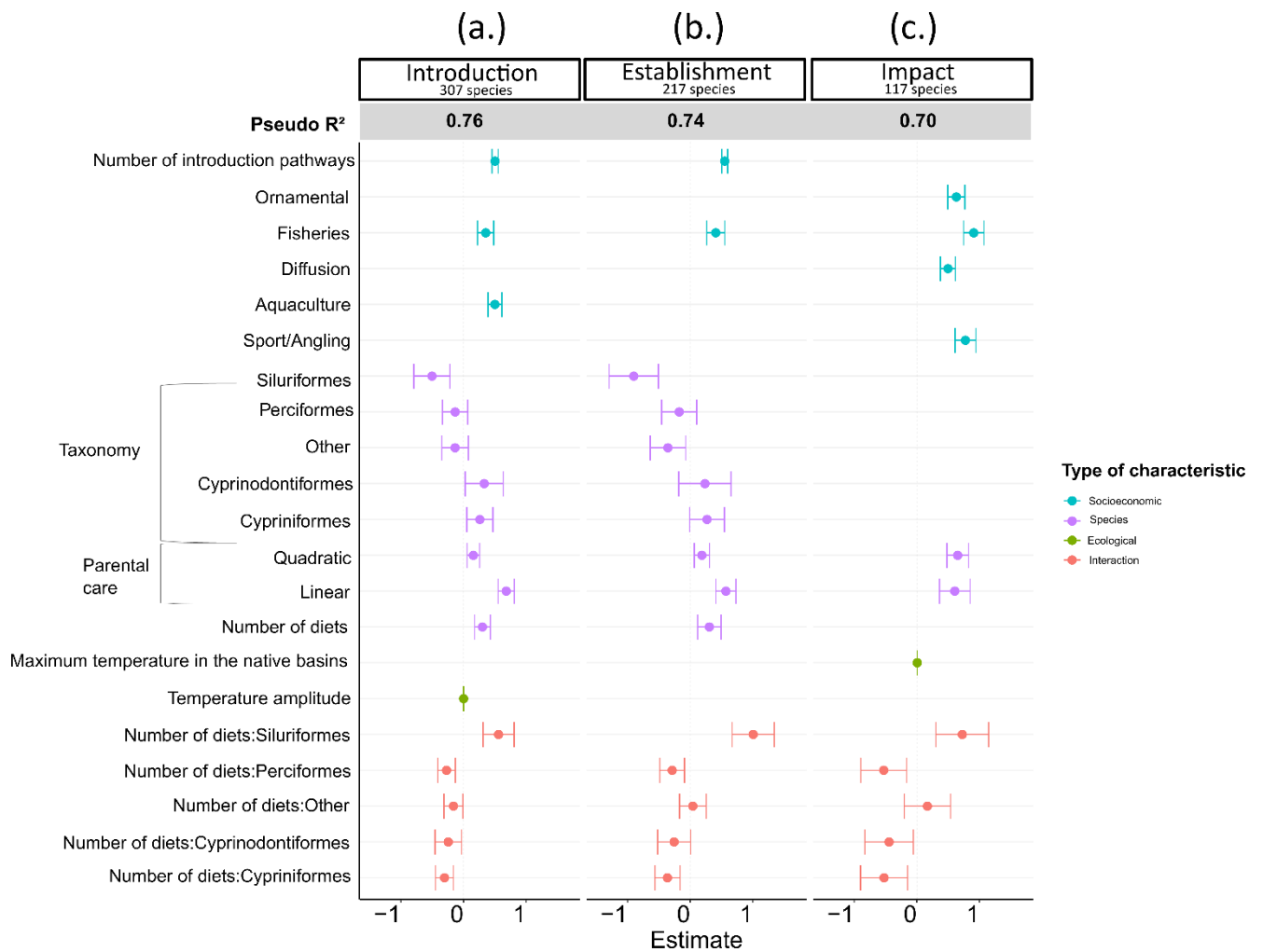
619 Vila-Gispert, A., Alcaraz, C., & García-Berthou, E. (2005). *Life-history traits of invasive fish*
620 *in small Mediterranean streams*. 7, 107-116. [10.1007/s10530-004-9640-y](https://doi.org/10.1007/s10530-004-9640-y)

621 Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., & Vanni, M. J. (2017). Functional ecology
622 of fish : Current approaches and future challenges. *Aquatic Sciences*, 79(4), 783-801.
623 <https://doi.org/10.1007/s00027-017-0546-z>

624 Vitule, J. R. S., Freire, C. A., & Simberloff, D. (2009). Introduction of non-native freshwater
625 fish can certainly be bad. *Fish and Fisheries*, 10(1), 98-108. <https://doi.org/10.1111/j.1467->
626 [2979.2008.00312.x](https://doi.org/10.1111/j.1467-2979.2008.00312.x)

627 Wonham, M. J., Carlton, J. T., Ruiz, G. M., & Smith, L. D. (2000). Fish and ships : Relating
628 dispersal frequency to success in biological invasions. *Marine Biology*, 136(6), 1111-1121.
629 <https://doi.org/10.1007/s002270000303>

630
631



632

633 Figure 1: Estimates (with standard errors) of significant variables resulting from the generalized linear

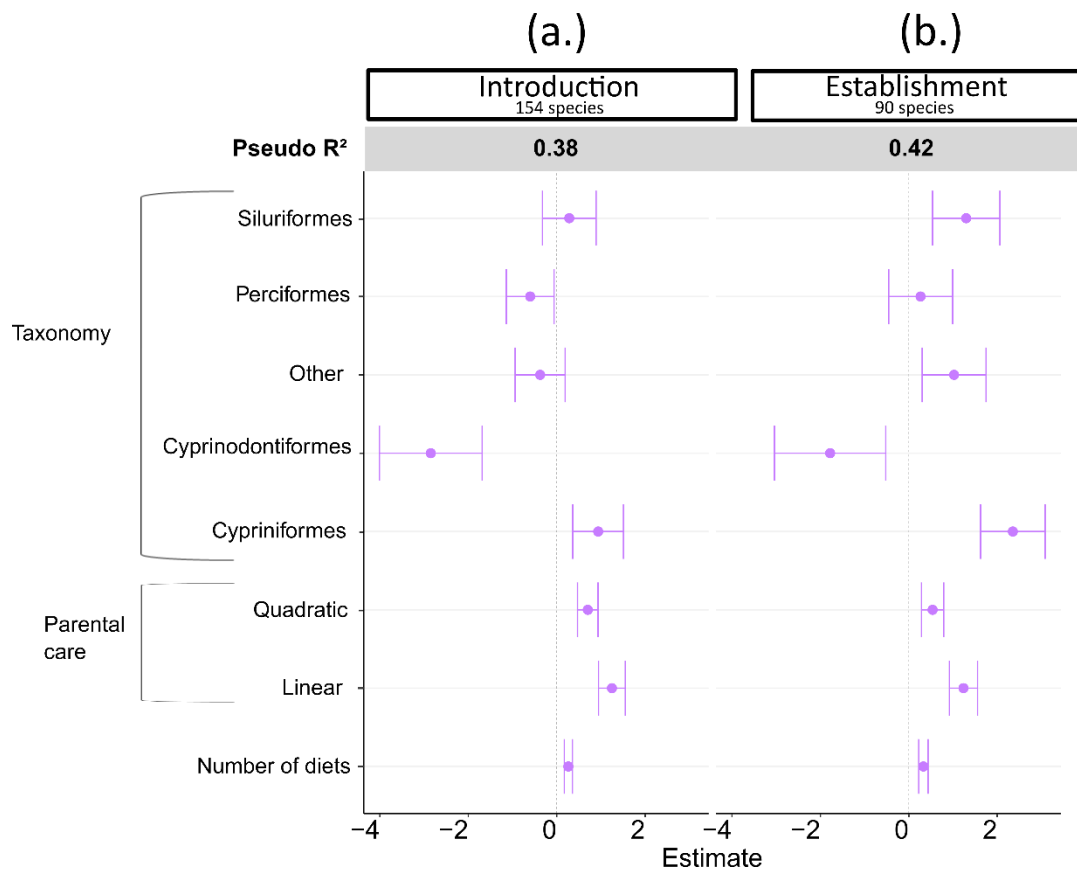
634 model for all the introduced species (Global) and for each step of the invasion. The sign of the correlation

635 depends on the category of reference for the Taxonomy and Major native bioregion variables. For

636 taxonomy, the reference is the Characiformes order. Introduction step intercept: 0.676 (SE = 0.209).

637 Establishment step intercept: 0.249 (SE = 0.305). Impact step intercept: -3.813 (SE = 1.036).

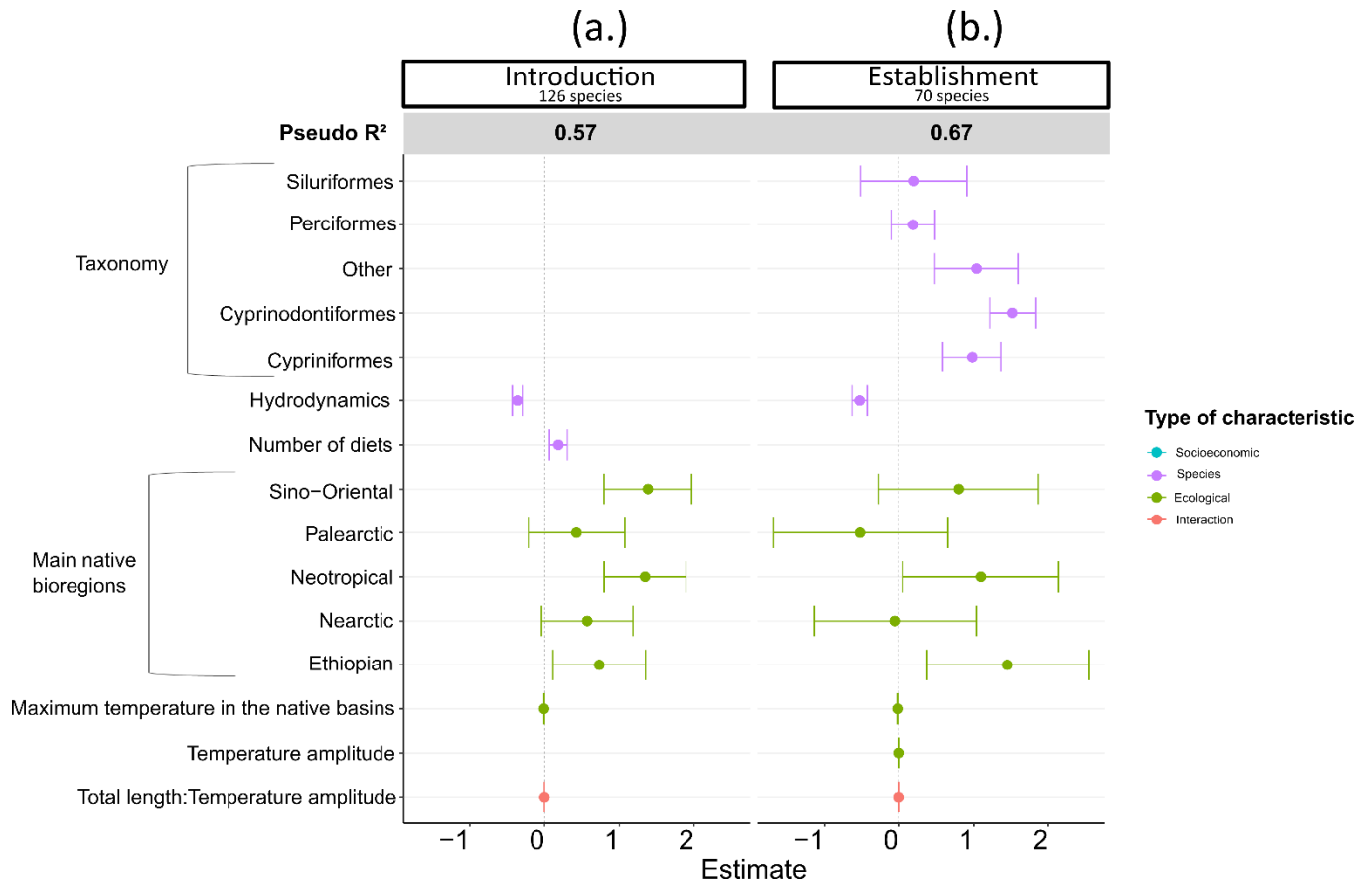
638



639

640 Figure 2: Estimates (with their standard errors) of significant variables resulting from the generalized
 641 linear model for the established species introduced through the aquaculture pathway and for the
 642 introduction and establishment steps. The sign of the correlation depends on the category of reference
 643 for the Taxonomy, Main diet, and Major native bioregion variables. For taxonomy, the reference is the
 644 Characiformes order. For diet, it is the detritus diet. Introduction step intercept: 2.367 (SE = 0.538).
 645 Establishment step intercept: -0.95 (SE = 1.227).

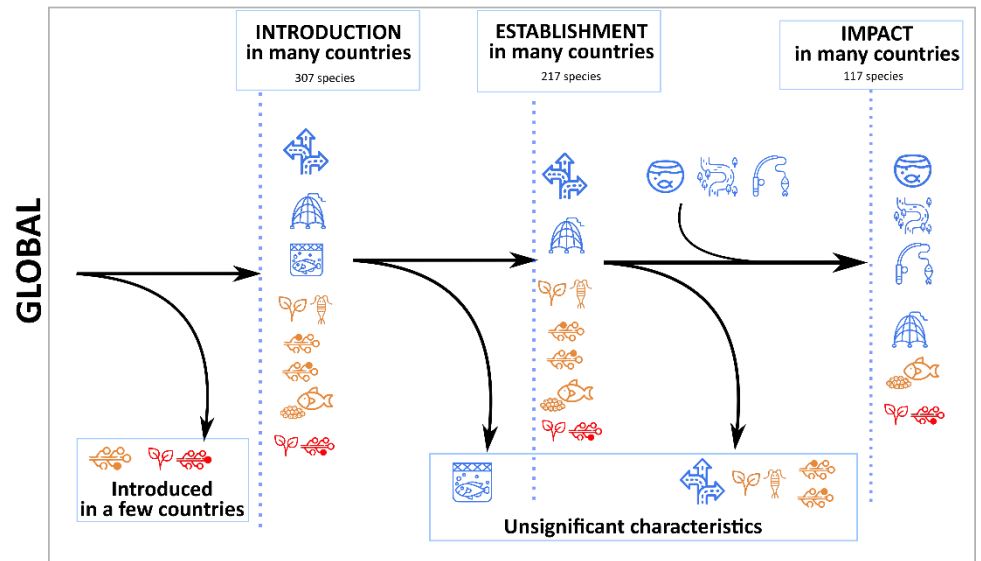
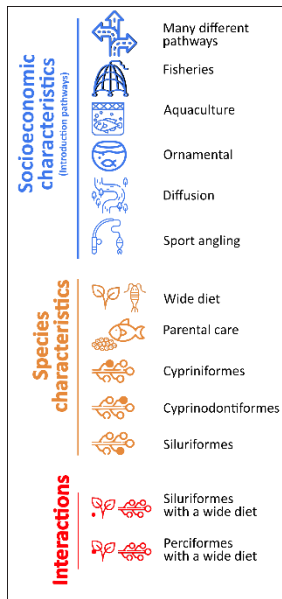
646



647

648 Figure 3: Estimates (with their standard errors) of significant variables resulting from the generalized
 649 linear model for the species introduced through the Ornamental pathway. The sign of the correlation
 650 depends on the category of reference for the Taxonomy and Major native bioregion variables. For the
 651 order, the reference is the Characiformes order. For the major native bioregion, the reference is the
 652 Australian region. Introduction step intercept: 1.752 (SE = 1.31). Establishment step intercept: 4.6 (SE
 653 = 1.9).

654



655

656 Figure 4: Main important characteristics favoring the success of each step of the invasion process.

657

Appendix 1: Reclassification of pathway categories

New pathway categories	FishBase pathway categories
Aquaculture	Aquaculture
Sport/Angling	Angling/Sport
Species control	Weed control – mosquito control – other pest control – phyto-zooplankton control – snail control
Diffusion	Lesseptian migration – spread from other countries – removal of natural barrier
Accidental	Accidental – accidental with ships
Fisheries	Fisheries
Ornamental	Ornamental
<i>Pathways not considered</i>	Unknown – no data – other reasons – bait – forage – fill ecological niche – off-site preservation – research

660 **Appendix 2: Countries and locations considered after reclassifying**

661 **locations**

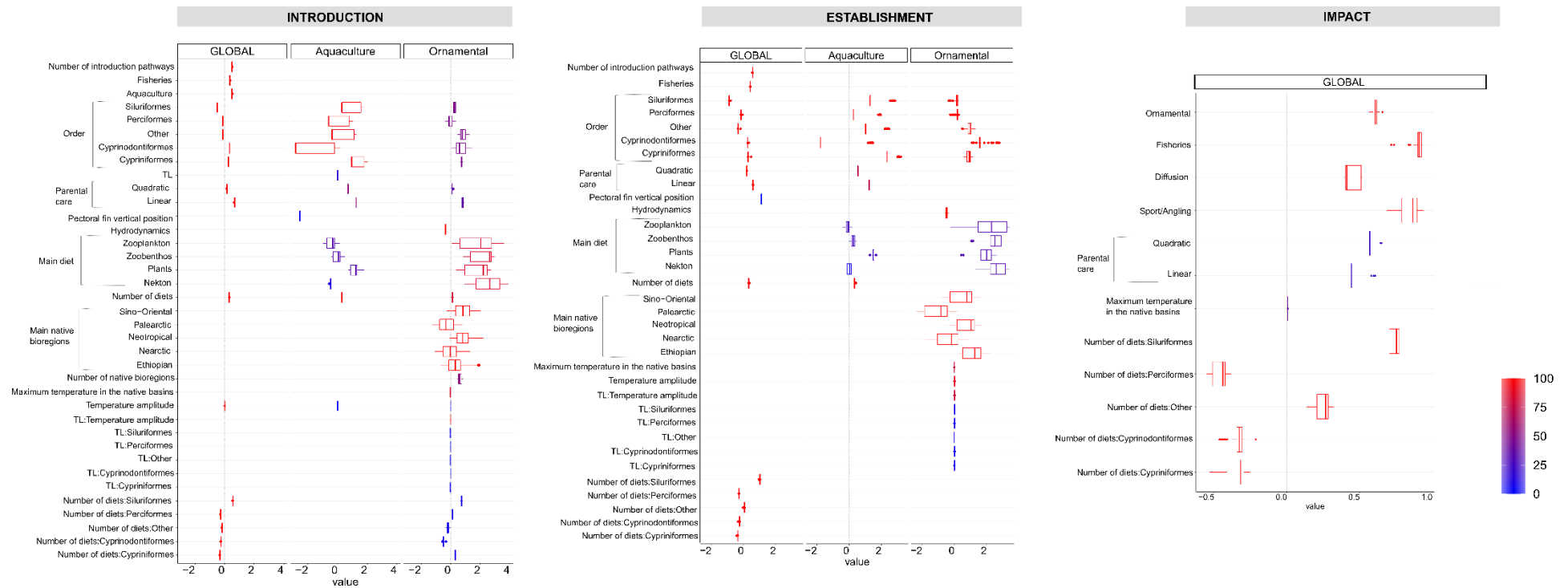
1	Afghanistan	41	Comoros	81	Hawaii	121	Mexico	161	Shanghai	201	Vanuatu
2	Alaska	42	Congo	82	Honduras	122	Moldova	162	Sierra Leone	202	Venezuela
3	Albania	43	Cook Islands	83	Hungary	123	Mongolia	163	Singapore	203	Vietnam
4	Algeria	44	Costa Rica	84	Iceland	124	Morocco	164	Slovakia	204	Wallis and Futuna
5	American Samoa	45	Cote d'Ivoire	85	India	125	Mozambique	165	Slovenia	205	Yemen
6	Angola	46	Croatia	86	Indonesia	126	Myanmar	166	Solomon Islands	206	Zaire
7	Antigua-and-Barbuda	47	Cuba	87	Iran	127	Namibia	167	South Africa	207	Zambia
8	Argentina	48	Curacao	88	Iraq	128	Nauru	168	South Korea	208	Zimbabwe
9	Armenia	49	Cyprus	89	Ireland	129	Nepal	169	Spain		
10	Australia	50	Czech Republic	90	Israel	130	Neth Antilles	170	Sri Lanka		
11	Austria	51	Czechoslovakia	91	Italy	131	Netherlands	171	St. Vincent and the Grenadines		
12	Azerbaijan	52	Denmark	92	Jamaica	132	New Caledonia	172	Sudan		
13	Azores Is.	53	Dominica	93	Japan	133	New Zealand	173	Suriname		
14	Bahamas	54	Dominican Republic	94	Kazakhstan	134	Nicaragua	174	Swaziland		
15	Bangladesh	55	East Timor	95	Kenya	135	Nigeria	175	Sweden		
16	Barbados	56	Ecuador	96	Kerguelen	136	Niue	176	Switzerland		
17	Belarus	57	Egypt	97	Kiribati	137	North Korea	177	Syria		
18	Belgium	58	El Salvador	98	Korea	138	Norway	178	Taiwan		
19	Belize	59	Eritrea	99	Kuwait	139	Oman	179	Tajikistan		
20	Benin	60	Estonia	100	Kyrgyzstan	140	Pakistan	180	Tanzania		
21	Bermuda	61	Ethiopia	101	Laos	141	Palau	181	Thailand		
22	Bhutan	62	Falkland Islands	102	Latvia	142	Panama	182	Tibet		
23	Bolivia	63	Federated States of Micronesia	103	Lebanon	143	Papua New Guinea	183	Togo		
24	Borneo	64	Fiji	104	Lesotho	144	Paraguay	184	Tonga		
25	Bosnia Herzegovina	65	Finland	105	Liberia	145	Peru	185	Torres Strait Islands		
26	Botswana	66	France	106	Libya	146	Philippines	186	Trinidad		
27	Brazil	67	French Guiana	107	Liechtenstein	147	Poland	187	Tunisia		
28	Brunei Darussalam	68	French Polynesia	108	Lithuania	148	Portugal	188	Turkey		
29	Bulgaria	69	Gabon	109	Luxembourg	149	Puerto Rico	189	Turkmenistan		
30	Burkina Faso	70	Galapagos Is.	110	Macedonia	150	Qatar	190	Tuvalu		
31	Burundi	71	Georgia	111	Madagascar	151	Reunion	191	Uganda		
32	Cambodia	72	Germany	112	Madeira Is.	152	Romania	192	UK		
33	Cameroon	73	Ghana	113	Malawi	153	Russia	193	Ukraine		
34	Canada	74	Greece	114	Malaysia	154	Rwanda	194	United Arab Emirates		
35	Caroline Island	75	Greenland	115	Maldives	155	Samoa	195	Unknown		
36	Cayman Is.	76	Grenada	116	Malta	156	Sao Tome and Principe	196	Uruguay		
37	Central African Republic	77	Guatemala	117	Mariana Islands	157	Saudi Arabia	197	US Virgin Islands		
38	Chile	78	Guinea	118	Marshall Islands	158	Serbia	198	USA		
39	China	79	Guyana	119	Martinique	159	Montenegro	199	USSR		
40	Colombia	80	Haiti	120	Mauritius	160	Seychelles	200	Uzbekistan		

Appendix 3: Variables used in each model

<p>Introduction – Global Establishment – Global Impact – Global</p>	<p>Life history traits Main diet Number of diets Hydrodynamics Pectoral fin vertical position Parental care Total Length Order</p> <p>Ecological characteristics Temperature amplitude in the native basins Maximum temperature in the native basins Main native bioregion Number of native bioregions</p>	<p>Socioeconomic characteristics Aquaculture Sport/Angling Accidental Ornamental Fisheries Diffusion Species control Number of introduction pathways Human use</p> <p>Interactions Between Temperature amplitude and TL Between Order and Number of diets Between Order and TL Between Ornamental and TL Between Sport/Angling and TL Between Aquaculture and TL</p>
<p>Introduction – Aquaculture Introduction – Ornamental</p> <p>Establishment – Aquaculture Establishment – Ornamental</p>	<p>Life history traits Main diet Number of diets Hydrodynamics Pectoral fin vertical position Parental care TL Order</p> <p>Ecological characteristics: Temperature amplitude in the native basins Maximum temperature in the native basins Main native bioregion Number of native bioregions</p>	<p>Interactions Between Temperature amplitude and TL Between Order and Number of diet Between Order and TL</p>

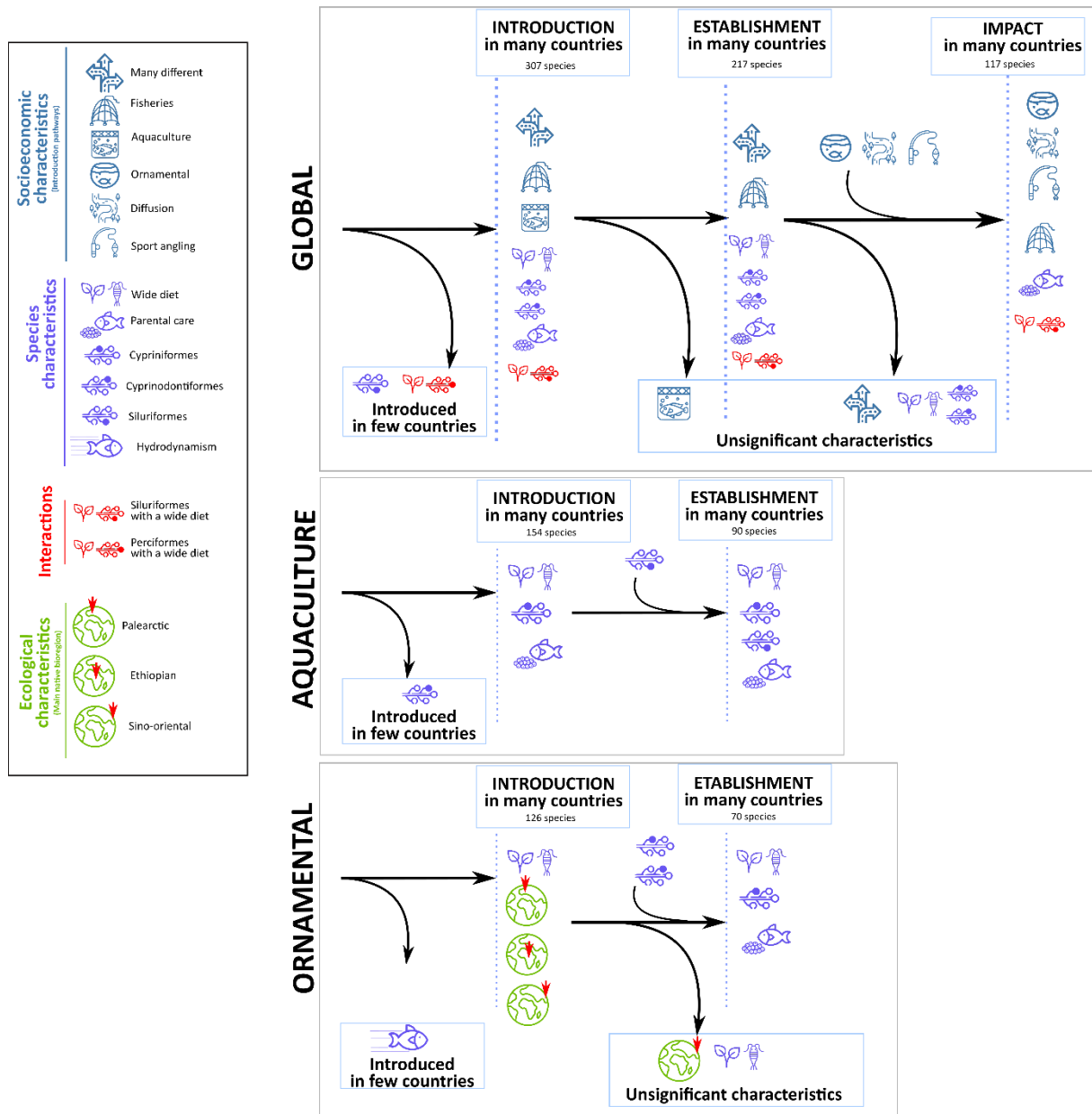
664 **Appendix 4: Sensitivity analysis**

665 Boxplots represent the estimates (without standard errors) of 100 models. We varied the main diet of species with several main diets and the main
 666 native bioregion of species with several main native bioregions. The color gradient represents the number of models in which the considered
 667 variable is significant (1: blue, 100: red). “TL” refers to total length.



669 **Appendix 5:** Main characteristics to succeed at each invasion step for the global pool and

670 for species introduced through the ornamental and aquaculture pathways



671

672

673

674 **Appendix 6: Differences in characteristics between introduced and** 675 **non-introduced species**

676 Methods

677 *Introduction status*

678 We took as introduced all species introduced to at least one location (i.e., species with at least
679 one location listed in the “TO” column of the *introduction()* table). It should be noted that some
680 species were simply imported to the location without being introduced to the wild. These
681 species were impossible to separate from others, although they represent only a very small part
682 of the data (Nicolas Bally, pers. com.). Thus, these were taken as species introduced to the wild.

683 *Statistical analysis*

684 To compare the characteristics of the introduced species with those of the non-introduced
685 species, we conducted univariate comparisons between the introduced and non-introduced
686 species for each characteristic. First, we directly compared introduced versus non-introduced
687 species. Second, we accounted for the class imbalance between non-introduced species
688 (majority class) and introduced species (minority class) by performing a repeated random sub-
689 sampling approach. In this latter approach, we reduced the majority class (non-introduced
690 species) to a random sample of size equal to the minority class (introduced species) and then
691 made 999 repetitions. To test the significance of the results, we used a Fisher test for each
692 modality when the considered characteristic was a qualitative variable and a Wilcoxon test for
693 quantitative variables. We considered a test to be significant when $p < 0.05$ (see Appendix 7 for
694 the p-values of each test).

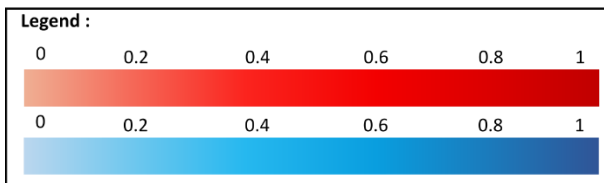
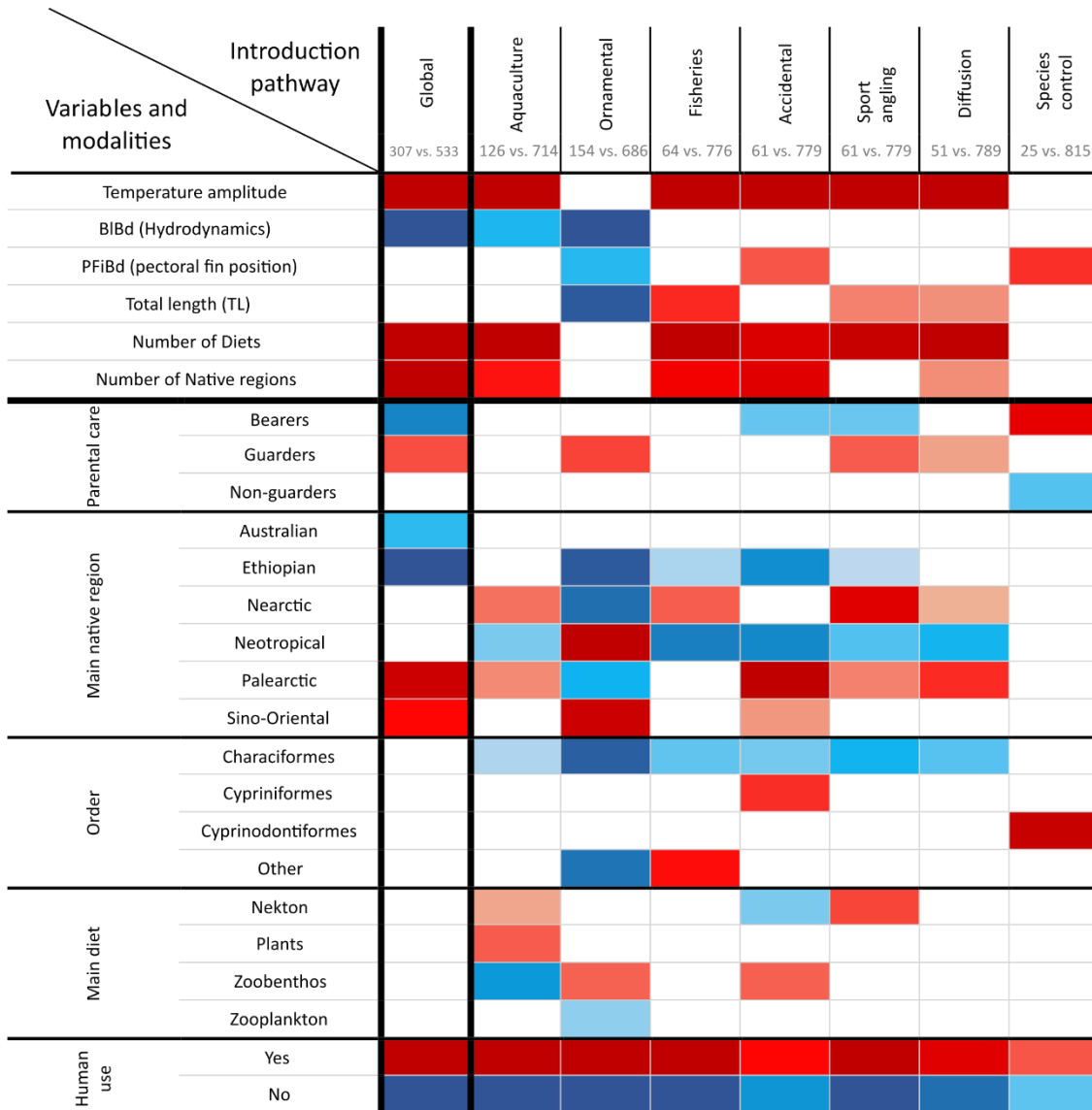
695 We performed these analyses for the entire pool of species and then specifically analyzed each
696 pathway in order to detect any interactions between pathways and species characteristics. As

697 the main diet and main native region of some species were chosen randomly from several
698 possibilities, we also performed sensitivity analysis on the main diet and main native region.
699 To do so, we randomly selected (100 repetitions) the main diet and main native region between
700 the different modalities for the concerned species.

701 **Results**

702 We examined the characteristics that were overrepresented in the introduced species pool
703 compared to the non-introduced pool of species (Fig. 1). We found that introduced species had
704 a higher temperature amplitude in their native basins, a higher number of diets and native
705 regions, and were more often used by humans than non-introduced ones. These differences
706 were found in the majority of the considered introduction pathways, except for the ornamental
707 and species control pathways.

708 In addition, the native regions of the introduced species strongly differed for the different
709 pathways (Fig. S1). For example, species mainly native to the Palearctic and Sino-Oriental
710 regions were more represented among introduced species than non-introduced ones in the
711 global pool. By contrast, the Neotropical region was more represented among species
712 introduced through the ornamental trade pathway compared to other species. Species
713 introduced by the ornamental pathway also had ventral pectoral fins and were rather small
714 (compared to long fish introduced by fisheries and sport/angling). Accidentally introduced
715 species tended to have lateral pectoral fins and were more represented in the Cypriniformes
716 order than other fish. Concerning species introduced by sport/angling, they were more
717 represented in the guarder strategy for parental care and in the nekton category for main diet
718 compared to other fish. Finally, species introduced for species control were more represented
719 in the bearer strategy for parental care, in the Cyprinodontiformes order, and had lateral pectoral
720 fins compared to other species.



721

722 *Figure S1: Results of Wilcoxon tests and F-tests per modality for each variable and each*
 723 *introduction pathway (see Appendix 7 for p-values). Red (blue) color indicates when introduced*
 724 *species are significantly more (less) represented or have a significantly higher (lower) value*
 725 *than non-introduced species using comparisons with all species. The gradient of colors*
 726 *represents the proportion of significant tests using the resample method. Only variables with a*
 727 *significant difference are presented. The p-values of tests with all species are available in the*
 728 *Appendix 7. It is important to note that these results do not describe the main characteristics of*

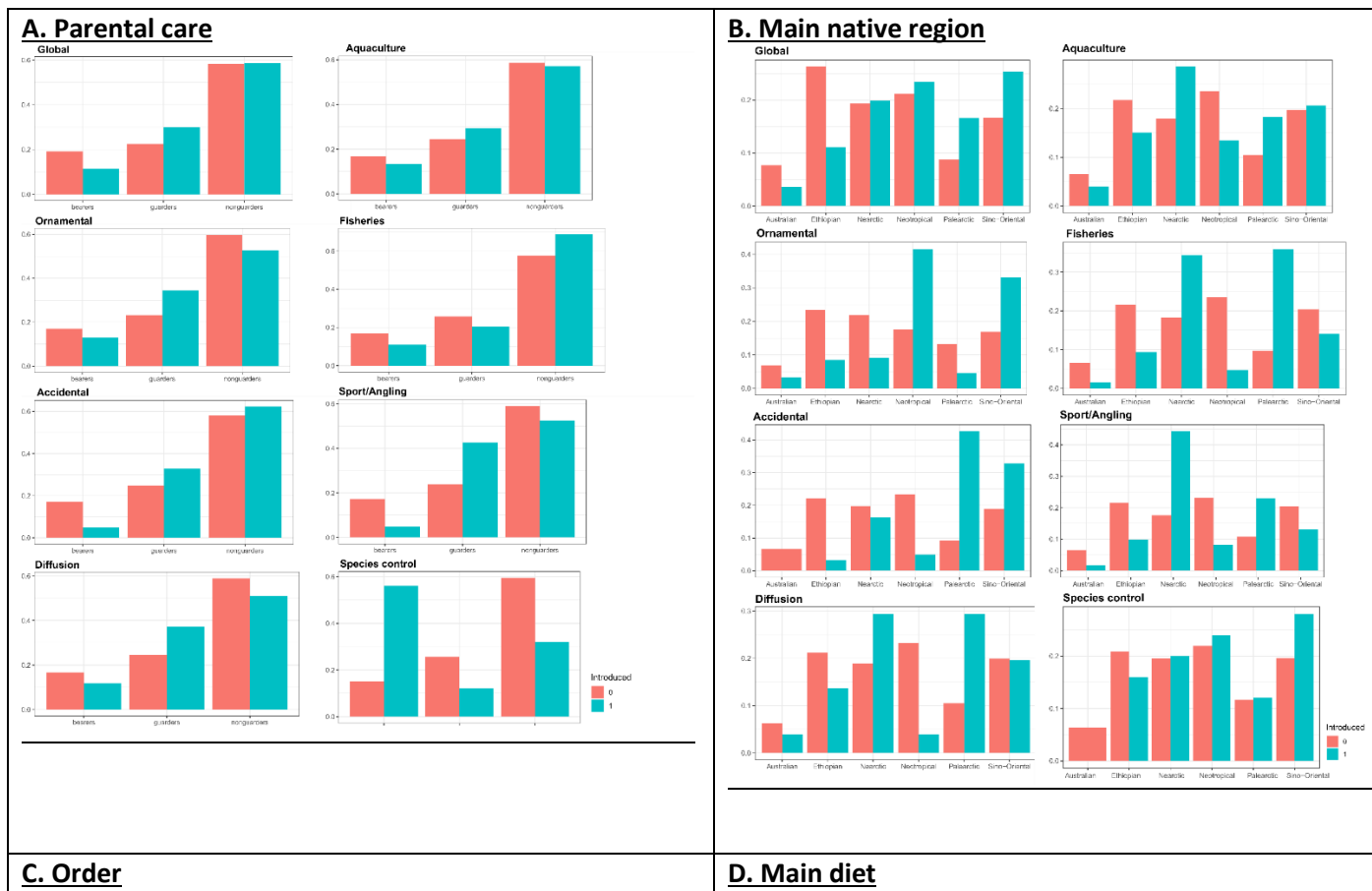
729 *the introduced species (see Appendix 6bis) but rather the differences between the introduced*
730 *and non-introduced species.*

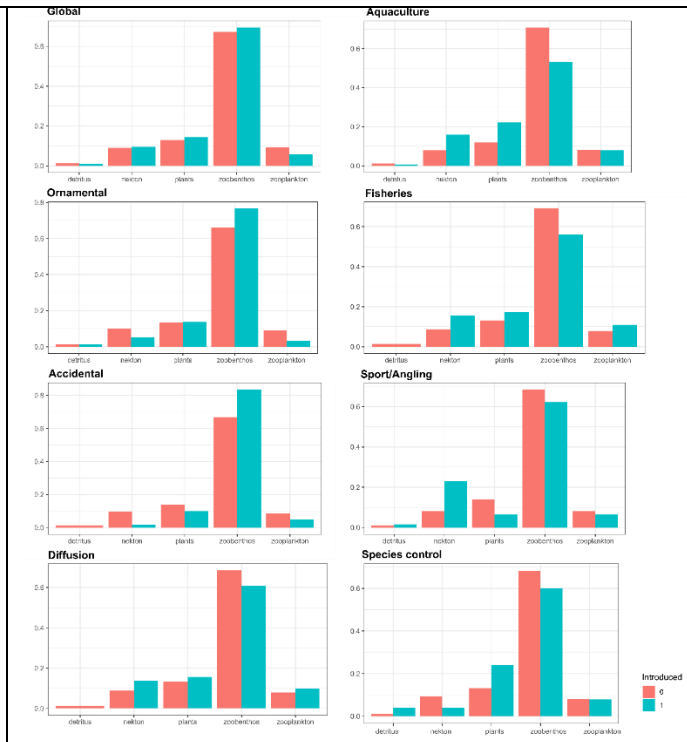
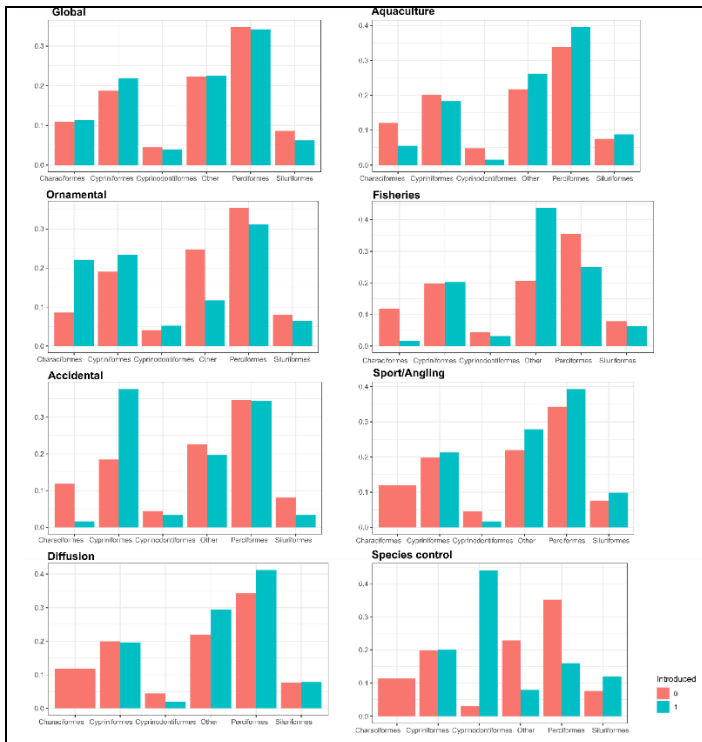
731 **Discussion**

732 We demonstrated the importance of a high number of diets and a high temperature tolerance to
733 differentiate introduced species from non-introduced ones at the global scale. These findings
734 are supported by the literature at the local scale (e.g., North America, Kolar and Lodge, 2002;
735 Parana River, Tonella et al., 2018). In addition, human use is unsurprisingly related to a greater
736 likelihood of introduction and has already been highlighted to differentiate invasive and native
737 species (Alcaraz et al., 2005). Moreover, species from a higher number of native regions were
738 also more introduced, perhaps because they have greater opportunities to be in contact with
739 human activities. Nonetheless, some species with only one native bioregion can also be
740 introduced in numerous countries: for example, the common carp (*Cyprinus carpio*), native to
741 the Sino-Oriental region, has the highest number of introduced countries in our pool (i.e. 133
742 countries).

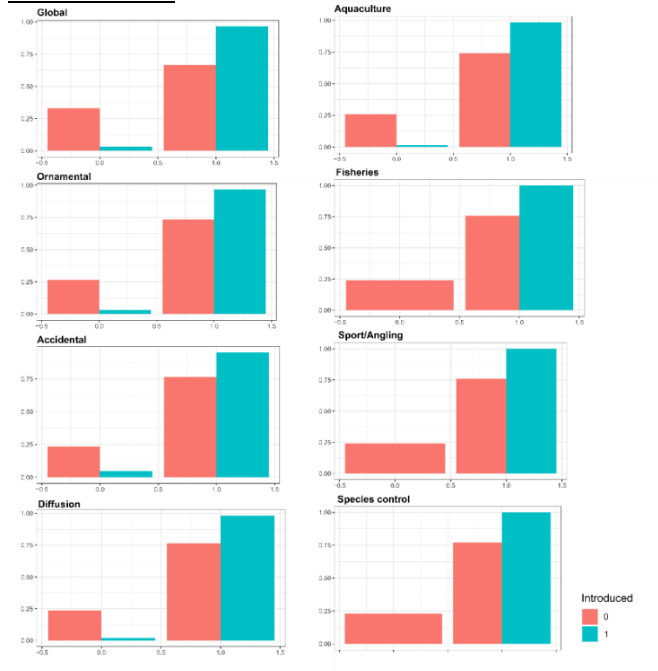
743 **Appendix 6bis: Representation of qualitative data**

744 Overall, successfully introduced species were mainly used by humans, adopted a non-guarder
 745 strategy for parental care, were represented by the Perciformes or Cypriniformes orders, and
 746 had a zoobenthos main diet. The only exceptions were for species introduced through the
 747 species control pathway. Species introduced for species control were mainly from the
 748 Cyprinodontiformes order and adopted a bearer strategy for parental care (Appendix 6bis, A,
 749 C, D, E). We found that species mainly native to the Sino-Oriental, Neotropical, and Nearctic
 750 regions were frequently introduced species (Appendix 6bis, B).





E. Human use



751

752

753

754 **Appendix 7: Results of Wilcoxon tests (A) and Fisher tests (B)**

755 The cells in white correspond to the p-values of the direct comparisons between introduced and non-introduced species for each characteristic. The
 756 cells in gray show the proportion of significant tests performed using the repeated random subsampling approach. With this latter approach, we
 757 reduced the majority class (non-introduced species) to a random sample of size equal to the minority class (introduced species) and performed 999
 758 repetitions.

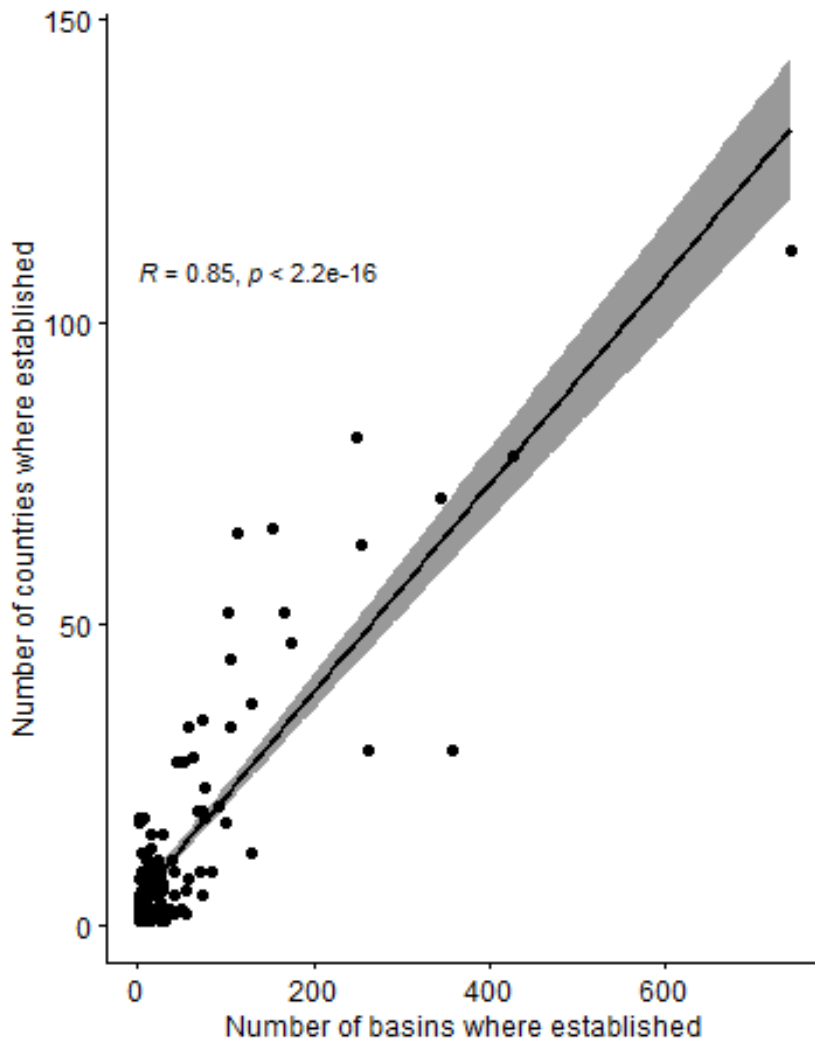
A.	Amplitudetemp		BIBd		TL		NbDiet		NbNativeRegion		PFiBd	
GLOBAL	2.51E-10	1	1.04E-06	1	0.737604	0	6.78E-12	1	0.000143	0.998999	0.485032	0.001001
Aquaculture	2.02E-11	1	0.002798	0.725726	0.07099	0.189189	1.74E-13	1	0.00031	0.820821	0.664508	0.014014
Species control	0.173449	0.066066	0.337548	0.049049	0.616464	0.021021	0.78624	0.001001	0.264231	0.072072	0.000931	0.685686
Ornamental	0.368074	0.032032	1.95E-11	1	2.21E-05	0.988989	0.053015	0.263263	0.152031	0.096096	0.003518	0.698699
Fisheries	6.85E-12	1	0.914416	0.005005	0.00101	0.723724	4.04E-08	0.997998	3.40E-06	0.922923	0.462093	0.038038
Accidental	9.54E-15	1	0.346491	0.036036	0.265602	0.057057	2.36E-05	0.95996	3.38E-07	0.954955	0.00684	0.515516
Sport angling	9.51E-10	1	0.483734	0.026026	0.024289	0.317317	2.36E-06	0.986987	0.055281	0.155155	0.831201	0.025025
Diffusion	2.60E-07	0.995996	0.928826	0.011011	0.044861	0.251251	6.97E-08	1	0.017359	0.263263	0.11614	0.111111

B.	Bearers		Guarders		Non-guarders		Detritus		Nekton		Plants		Zoobe
GLOBAL	0.003544	0.905906	0.020779	0.548549	0.942193	0	0.754013	0	0.732406	0	1	0	0.298897
Aquaculture	0.432483	0.009009	0.266134	0.021021	0.769127	0.008008	1	0	0.030585	0.145145	0.005761	0.492492	0.000293
Species control	4.53E-06	0.937938	0.160819	0.04004	0.011815	0.372372	0.261987	0	1	0	0.163433	0.066066	0.293126
Ornamental	0.230178	0.027027	0.005401	0.597598	0.104478	0.131131	1	0	0.062202	0.193193	1	0.002002	0.012419

Fisheries	0.290759	0.023023	0.453784	0.009009	0.087399	0.112112	1	0	0.098381	0.078078	0.59911	0.001001	0.058526
Accidental	0.010633	0.484484	0.169103	0.038038	0.590419	0.009009	1	0	0.009727	0.421421	0.369087	0.016016	0.008623
Sport angling	0.010633	0.481481	0.002016	0.488488	0.346531	0.025025	0.531461	0	0.000393	0.587588	0.074201	0.135135	0.338183
Diffusion	0.438486	0.014014	0.046671	0.167167	0.305122	0.02002	1	0	0.249888	0.014014	0.8451	0.002002	0.231947
	Australian		Ethiopian		Nearctic		Neotropical		Palearctic		Sino-Oriental		Human u
GLOBAL	0.014608	0.680681	1.35E-07	1	0.856894	0	0.489266	0.002002	0.001116	0.980981	0.00432	0.878879	1.80E-28
Aquaculture	0.413994	0.007007	0.119417	0.094094	0.007232	0.386386	0.013894	0.415415	0.01604	0.284284	0.905013	0.001001	1.05E-12
Species													0.002570427
control	0.392562	0.002002	0.801416	0.001001	1	0	0.807353	0.001001	1	0	0.319174	0.022022	
Ornamental	0.058244	0.203203	1.39E-05	0.985986	0.00018	0.952953	1.29E-09	1	0.001306	0.778779	1.30E-05	0.976977	1.24E-12
Fisheries	0.167867	0.047047	0.02303	0.263263	0.004606	0.477477	0.000129	0.921922	8.82E-08	0.990991	0.257193	0.037037	6.54E-08
Accidental	0.043255	0.168168	0.000113	0.893894	0.616514	0.006006	0.000311	0.896897	1.08E-10	1	0.019535	0.224224	0.000318095
Sport angling	0.252548	0.025025	0.031938	0.203203	4.83E-06	0.947948	0.00577	0.564565	0.010836	0.315315	0.185659	0.058058	1.84E-07
Diffusion	0.761908	0	0.282508	0.03003	0.070263	0.103103	0.000393	0.75976	0.00032	0.711712	1	0.001001	4.05E-05
	Characiformes		Cypriniformes		Cyprinodontiformes		Other		Perciformes		Siluriformes		
GLOBAL	0.820158	0	0.28317	0.016016	0.727339	0	1	0	0.880377	0	0.228691	0.008008	
Aquaculture	0.03098	0.251251	0.716595	0.001001	0.148842	0.068068	0.296494	0.027027	0.222938	0.044044	0.592005	0.001001	
Species													
control	0.099416	0.05005	1	0	5.24E-10	0.994995	0.090298	0.1001	0.054311	0.135135	0.433603	0	
Ornamental	1.18E-05	0.978979	0.263526	0.024024	0.512046	0.002002	0.000259	0.937938	0.349136	0.02002	0.618217	0.002002	
Fisheries	0.006354	0.506507	0.87193	0	1	0.001001	6.87E-05	0.852853	0.10166	0.095095	0.809885	0.001001	
Accidental	0.009741	0.444444	0.000722	0.698699	1	0	0.749652	0.006006	1	0.001001	0.219148	0.02002	
Sport angling	0.001034	0.772773	0.740696	0.006006	0.507933	0.006006	0.337598	0.026026	0.484922	0.019019	0.460308	0.004004	
Diffusion	0.004267	0.541542	1	0.002002	0.718426	0.001001	0.225614	0.051051	0.362274	0.012012	1	0	

760

761 **Appendix 8: Correlation between the number of countries and the**
762 **number of basins where species have established (161 species**
763 **considered)**



764

765

766

767 **References :**

768 Alcaraz, C., Vila-Gispert, A., & García-Berthou, E. (2005). Profiling invasive fish species : The
769 importance of phylogeny and human use: Profiling invasive fish. *Diversity and Distributions*, 11(4),
770 289-298. <https://doi.org/10.1111/j.1366-9516.2005.00170.x>

771

772 Kolar, C. S., & Lodge, D. M. (2002). Ecological Predictions and Risk Assessment for Alien Fishes in
773 North America. *Science*, 298(5596), 1233-1236. <https://doi.org/10.1126/science.1075753>

774

775 Tonella, L. H., Fugi, R., Vitorino, O. B., Suzuki, H. I., Gomes, L. C., & Agostinho, A. A. (2018).

776 Importance of feeding strategies on the long-term success of fish invasions. *Hydrobiologia*, 817(1),

777 239-252. <https://doi.org/10.1007/s10750-017-3404-z>

778