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1 **Knowledge gaps in economic costs of invasive alien fish worldwide**

2

3 Running head: Costs of fish invasions

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37 **Highlights:**

- 38 ● Invasive alien fish species have cost at least \$37.08 billion globally since 1960s
- 39 ● Annual costs increased from < \$0.01 million in the 1960s to \$1 billion since 2000
- 40 ● Reported costs are unevenly distributed, with a bias towards North America
- 41 ● Impacts are less reported than other taxa based on research effort
- 42 ● Gaps in available data indicate underestimation and a need to improve cost reporting

43

44

45 **Abstract**

46 Invasive alien fishes have had pernicious ecological and economic impacts on both aquatic
47 ecosystems and human societies. However, a comprehensive and collective assessment of
48 their monetary costs is still lacking. We reviewed reported data on the economic impacts of
49 invasive alien fishes using InvaCost, the most comprehensive global database of invasion
50 costs, and analysed how total (i.e. observed and potential/predicted) and observed (i.e.
51 empirically incurred) costs of fish invasions are distributed geographically and temporally and
52 assessed which socioeconomic sectors are most affected. Fish invasions have potentially
53 caused the economic loss of at least US\$37.08 billion globally, from just 27 reported species.
54 North America reported the highest costs (>85% of the total economic loss), followed by
55 Europe, Oceania and Asia, with no costs yet reported from Africa or South America. Only
56 6.6% of the total reported costs were from invasive alien marine fish. Costs that were
57 observed amounted to US\$2.28 billion (6.1% of total costs), indicating that costs of damages
58 caused by invasive alien fishes are often extrapolated and/or difficult to quantify. Most of the
59 observed costs were related to damage and resource losses (89%). Observed costs mainly
60 affected public and social welfare (63%), with the remainder borne by fisheries, authorities
61 and stakeholders through management actions, environmental, and mixed sectors. Total costs
62 have increased significantly over time, from <US\$0.01 million/year in the 1960s to over
63 US\$1 billion/year in the 2000s, and observed costs have followed a similar trajectory. Despite
64 the growing body of work on fish invasions, information on costs has been much less than
65 expected, given the overall number of invasive alien fish species documented and the high
66 costs of the few cases reported. Both invasions and their economic costs are increasing,
67 exacerbating the need for improved cost reporting across socioeconomic sectors and
68 geographic regions, for more effective management.

69

70 **Keywords:** biodiversity conservation; fisheries; InvaCost; marine and freshwater; non-native
71 species; socio-economic damages

72

73 **Introduction**

74 Invasive alien fish introductions are increasing in number globally (Leprieur et al., 2008;
75 Avlijaš et al., 2018). In turn, the drivers of these invasions are also rising (Turbelin et al.,
76 2017; Zieritz et al., 2017), with the potential to intensify future impacts. In particular, the
77 increase in anthropogenic activities, especially in emerging market economies, is expected to
78 facilitate new introductions of invasive alien fish species and subsequent invasions through
79 pathways such as tourism, trade (e.g. aquaculture and aquarium trade) and infrastructure
80 development (e.g. waterways/channel construction) (Hulme, 2015; Haubrock et al., 2021a).

81 Ecological impacts of invasive alien fishes (Cucherousset & Olden, 2011) include the
82 displacement and extinction of native species (Mills et al., 2004; Haubrock et al., 2018),
83 alteration of trophic interactions (Martin et al., 2010; Cuthbert et al., 2018; Haubrock et al.,
84 2019), and disruption of ecosystem functioning (Capps & Flecker, 2013). Invasive alien fish
85 can also transmit new pathogens (Gozlan et al., 2005; Waicheim et al., 2014; Boonthai et al.,
86 2017; Ercan et al., 2019) and threaten native species' genetic diversity through hybridization
87 (Oliveira et al., 2006; Gunnell et al., 2007). However, despite evidence for increasing
88 numbers of fish invasions worldwide and their growing ecological impacts (Leprieur et al.,
89 2008; Seebens et al., 2020; Raick et al., 2020), their economic impacts remain poorly
90 understood, largely due to a lack of data for numerous sectors and difficulties in monetizing
91 ecological impacts. This paucity of cost data has led to debate among scientists about previous
92 estimates of invasion costs (Cuthbert et al., 2020), which have often relied on over-
93 extrapolation and presented untraceable sources. In the context of fisheries, this could involve
94 projecting costs from local scales to entire fisheries.

95 This lack of knowledge of costs of invasive alien fish, in turn, hampers decision-making and
96 severely limits the ability of policymakers to design cost-effective management strategies
97 (Britton et al., 2010; Hyytiäinen et al., 2013). In cases where invasive alien fish populations
98 may have a positive value, understanding the trade-offs and designing socially optimal
99 management are also hampered by the lack of cost data. Examples of such positive values
100 include invasive alien fishes with commercial benefits (Gollasch & Leppäkoski, 1999),
101 aesthetic and/or cultural values associated with recreational uses (Downing et al., 2013,
102 Schlaepfer et al., 2011, Katsanevakis et al., 2014, Gozlan 2015, 2016), or other perceived
103 ecosystem benefits (Gozlan, 2008; Pejchar & Mooney, 2009; Britton & Orsi, 2012).

104 Despite the potential benefits of some taxa, recent works have highlighted the increasing
105 negative economic impacts of invasive alien species globally (Bradshaw et al., 2016), with
106 economic costs of invasions exceeding US\$1.2 trillion in recent decades across all habitat
107 types (Diagne et al., 2021). In a first global synthesis of the cost of aquatic invasive alien
108 species, impacts have reached \$345 billion worldwide, which is likely an underestimate given
109 that impacts of aquatic invasions are generally under-represented compared to terrestrial taxa.
110 That is because their costs are lower than expected based on numbers of alien species between
111 those habitats (Cuthbert et al., 2021). Further, Cuthbert et al. (2021) found that the ruffe
112 *Gymnocephalus cernua* was the second most costly invasive aquatic taxon in the world,
113 considering total costs which include predictions and extrapolations. In addition, significant
114 gaps in reporting on the costs of aquatic invasions were found in Asia and Africa, with many
115 countries reporting no invasion costs, despite the presence of known harmful invasive alien
116 species (Cuthbert et al., 2021). While the increasing economic impacts of aquatic invasions
117 are alarming, there remain knowledge gaps at more granular scales regarding the specific
118 nature of impacts of key taxonomic groups, such as fish, which must be filled to fully
119 understand biases and inform taxon-specific management (Haubrock et al., 2021b; Cuthbert et
120 al., 2021; Kouba et al., 2021).

121 Following recent advances addressing costs of invasive alien species at different regional
122 scales (Bradshaw et al., 2021; Crystal-Ornelas et al., 2021; Haubrock et al., 2021c;
123 Kourantidou et al., 2021; Liu et al., 2021) and across taxonomic groups (Cuthbert et al.,
124 2021), we aim to better understand costs of fish invasions. To provide a necessary baseline for
125 the economic impact of this taxon, we have therefore characterised, for the first time, the
126 current status of knowledge on the global costs of invasive alien fishes using the InvaCost
127 database (Diagne et al., 2020a). This database contains detailed information on reported costs
128 (e.g. types of costs, sectors affected, regional attributes, reliability of cost estimates, etc.) over
129 the last 60 years, associated with ~ 1000 invasive alien species from all ecosystem types
130 worldwide (i.e. impacts occurring outside their native range). Invasive alien species included
131 in the InvaCost database are thus those that spread outside of their geographic range of origin
132 (Blackburn et al., 2011) and have a negative economic impact that was quantified in monetary
133 terms. Our aims were to describe the reported global costs associated with invasive alien fish
134 species, to explore the structure of these costs, and to identify gaps and potential biases in the
135 estimation of past and current economic impacts.

136

137 **Methods**

138 *Cost data sourcing and filtering*

139 To estimate the cost of fish invasions reported globally, we considered cost data from the
140 latest version of the InvaCost database (version 4.0,
141 <https://doi.org/10.6084/m9.figshare.12668570>; released in June 2021). This version of the
142 database compiles 13,123 cost entries reported from both English and non-English sources in
143 a sufficiently detailed manner to allow a large-scale synthesis of the costs associated with
144 invasive alien species at different spatial, taxonomic and temporal scales (Diagne et al.,
145 2020a; Angulo et al., 2021). These cost data were primarily retrieved using a series of search
146 strings entered into the Web of Science platform (<https://webofknowledge.com/>), Google

147 Scholar database (<https://scholar.google.com/>) and the Google search engine
148 (<https://www.google.com/>) to identify and collate relevant references on invasion costs. Local
149 stakeholders and experts on invasions were also contacted as part of the search process. All
150 references were thoroughly evaluated to identify their relevance and to extract information on
151 costs. In the invasive alien species literature, there is a wide variety of costing practices which
152 have an associated risk of misunderstandings and causing discrepancies among reported costs
153 (Diagne et al., 2021). These may include, for example, differences in discounting across
154 studies or in cost estimation methodologies. Despite the obvious challenges of standardizing
155 heterogeneous costs, InvaCost is the most comprehensive database on the economic costs of
156 IAS that has largely succeeded in resolving the problems associated with standardisation over
157 time and across countries where they have been reported (Diagne et al., 2020b). In addition,
158 this database is public and regularly updated with either corrections if mistakes are detected
159 and/or new data as they become available. With regard to monetary units, all costs published
160 in the literature and included in the database were converted to 2017 US\$ values (see Diagne
161 et al., 2020a and Supplementary Material 1 for detailed information). The database used for
162 this analysis includes information on monetary costs across taxonomic, regional and sectoral
163 descriptors, and allows for a distinction between *observed* (i.e. costs of a realized impact) and
164 *potential* costs (i.e. costs of a predicted/expected impact over time within or beyond the actual
165 distribution area of the IAS). It also allows for a classification based on the reliability of the
166 source and the methodologies used for the cost estimates (*high* or *low* reliability, with *high*
167 implying that the source is from pre-assessed material such as peer-reviewed articles and
168 official reports or from grey material but with documented, repeatable and traceable methods,
169 and with *low* referring to all other estimates).

170 We filtered the InvaCost database to retain costs related to fishes belonging to the classes
171 Cephalaspidomorphi and Actinopterygii; these were the only fish taxa in the database with
172 reported costs, but also included an entry listed as “Osteichthyes” (see Pimentel et al., 2000).

173 Because the available information did not allow us to distinguish this entry among ray-finned
174 fish (Actinopterygii) and lobe-finned fish (Sarcopterygii), it was kept as a “diverse” entry. In
175 total, we identified 177 entries, from which 7 were excluded as no starting and / or ending
176 year for the listed costs could be identified. After expansion, these entries resulted in 384
177 annualized cost entries (see expansion process below). Cost entries that were not attributable
178 to single species, sectors or cost types within these classes were classified as
179 “Diverse/Unspecified”. All analyses were conducted for the period between 1960 to 2020, as
180 (i) monetary exchange rates prior to 1960 were not available, and (ii) 2020 was the last year
181 for which cost data were available in the database. The final dataset used for the analysis is
182 provided in Supplementary Material 2.

183

184 *Global cost descriptions*

185 In order to describe the costs of invasive alien fish over time, we used the *expandYearlyCosts*
186 function of the ‘invacost’ package (v0.3-4; Leroy et al., 2020) in R version 4.0.2 (R Core
187 Team, 2020). This function facilitates consideration of the temporal dimensions of the data,
188 with the estimated costs per year being expanded over time according to the length of time
189 over which they occurred or were expected to have occurred (i.e. the length of time between
190 the *Probable_starting_year_adjusted* and *Probable_ending_year_adjusted* columns). In order
191 to obtain a comparable cumulative total cost for each estimate over the period during which
192 costs were incurred for each invasion, we multiplied each annual estimate by the respective
193 duration (in years). The analyses were therefore conducted on the basis of these ‘expanded’
194 entries to reflect the likely duration of the costs as reported in each study analysed. This
195 means that costs covering several years (e.g. US\$10 million between 2001 and 2010) are
196 divided according to their duration (i.e. US\$1 million for each year between 2001 and 2010).
197 Finally, the cumulative costs of the invasion were estimated based on their classification in

198 the following cost descriptors (i.e. columns) included in the database (Supplementary Material
199 1):

200 (i) *Method_reliability*: indicating the perceived reliability of cost estimates based on
201 the publication type and estimation method. Costs are considered to be of *low* reliability in
202 those cases where they were derived from grey literature and/or are lacking documented,
203 repeatable or traceable methods. On the contrary, costs are considered of *high* reliability if
204 they come from peer-reviewed articles, official documents, or grey literature but with a fully
205 documented, repeatable and traceable method (Diagne et al., 2020a). While we acknowledge
206 that this binary classification does not capture the widely varying methodologies of
207 underlying studies, it provides a practical, reproducible and objective means of cost
208 assessment and filtering;

209 (ii) *Implementation*: whether the cost estimate was actually incurred in the invaded
210 area (*observed*; e.g. a cost directly incurred from investment in managing an invasive alien
211 fish population, or an invasion-driven decline in a native fishery that resulted in a realised loss
212 of income) or whether it was extrapolated or predicted over time within or beyond the actual
213 distribution area of the IAS (*potential*), and thus not empirically incurred (Diagne et al.,
214 2020a; see Supplementary Material 1). We emphasize that costs were compiled in InvaCost
215 based on the information in each cost document (i.e. we did not extrapolate or predict cost
216 estimates independently here, and simply compiled reported costs). For example, *potential*
217 costs may include estimated reductions in fisheries income because of an invasion (Scheibel
218 et al., 2016), known local costs that are extrapolated to a larger system than the one they
219 occur in (Oreska and Aldridge, 2011), and costs extrapolated over several years based on
220 estimates from a shorter period (Leigh, 1998).

221 (iii) *Geographic_region*: description of the continental geographic location of the cost;

222 (iv) *Type_of_cost_merged*: grouping of costs into categories: (i) “*Damage*” referring
223 to damages or loss incurred by the invasion (i.e. costs of repairing damage, losses of

224 resources, medical care), (ii) “*Management*” including expenditure related to control (i.e.
225 surveillance, prevention, management, eradication), (iii) and “*Mixed*” including mixed cost of
226 damage and control (cases where the reported costs were not clearly distinguishable);

227 (v) *Impacted_sector*: the activity, societal or market sector that was affected by the
228 cost. Seven sectors are described in the database: *agriculture*, *authorities-stakeholders*
229 (official structures allocating efforts to manage biological invasions), *environment*, *fishery*,
230 *forestry*, *health*, and *public and social welfare* (Diagne et al., 2020a; see Supplementary
231 Material 1).

232

233 *Temporal cost accumulations*

234 To assess temporal trends of invasive alien fish species, we considered 10-year averages since
235 1960. We examined the costs in terms of the *year of impact*, which reflects the time at which
236 the invasion cost likely occurred and extended it over years in which the costs were realised
237 using the *summarizeCosts* function of the ‘*invacost*’ R package (using the
238 *Probable_starting_year_adjusted* and *Probable_ending_year_adjusted* columns; see Leroy et
239 al., 2020). This allowed the estimation of average annual costs over the whole period
240 considered, as well as over decadal increments, for both *observed* and *potential* costs.

241

242 *Comparison with other taxonomic groups*

243 In order to put the costs of invasive alien fish species in a broader taxonomic perspective, we
244 compared the economic costs of invasive alien fish with other invasive vertebrates: birds and
245 mammals. The comparison was based on the total cost and the number of documents
246 reporting costs in the InvaCost database, coupled with the number of invasive alien species
247 per taxon, and the numbers of scientific publications in the field of invasion science. First,
248 total monetary costs and number of entries for birds and mammals were calculated following
249 the same methods and database version as for fishes (as detailed above). Secondly, we

250 estimated the number of publications available for each group using the same search protocol
251 as for the InvaCost database (see Diagne et al., 2020a), excluding words referring to costs and
252 adding the name of the biotic group (i.e. “fish”, “mammal”, or “bird”), in order to obtain a
253 comparative approximation of the research effort in invasion ecology for these three taxa. The
254 exact search strings used can be found in Supplementary Material 3. The information
255 considered in this comparison was collected using the Web of Science Core collection.
256 Thirdly, the numbers of alien species for each of the three taxonomic groups mentioned above
257 was estimated using the IUCN Red List database (<https://www.iucnredlist.org/>). We classified
258 a species as alien according to the IUCN legends of the countries where they occur. If a
259 species is considered as introduced in at least one country, then we consider this species as
260 alien. Finally, we used Pearson’s Chi-squared test of independence to assess whether the data
261 for the three taxonomic groups had the same distribution of values (number of alien species,
262 number of cost entries, number of studies reporting invasion costs, and total costs).

263

264 **Results**

265 A total of 384 annualized cost entries for 27 invasive alien species belonging to 18 fish
266 families were available in the database, totalling US\$37.08 billion. The majority of costs was
267 deemed as potential (US\$34.79 billion; $n = 88$, hereafter the number of cost entries), while
268 observed costs amounted to only US\$2.28 billion ($n = 296$). Furthermore, the majority of
269 costs (US\$25.31 billion; $n = 295$) were considered of high reliability, while US\$11.77 billion
270 ($n = 89$) were considered of low reliability (Supplementary Material 4).

271

272 *Costs across regions and taxa*

273 North America was the region with the highest reported economic costs of invasive alien fish
274 species, followed by Europe, Oceania , Asia and Central America (Figure 1). Costs inferred

275 from polar regions (e.g. French Southern and Antarctic Lands) were below US\$ 1 million (no
276 costs for invasive alien fish were reported for Arctic regions).

277 When considering only observed costs, the costs of invasive alien fish in North
278 America ($n = 46$), were again about 10 times higher than observed costs recorded in Oceania
279 ($n = 12$), and over 60 times higher than costs in Asia ($n = 59$; Figure 2). Reported observed
280 costs were attributed to several species in North America, Europe and Asia, but were least
281 diverse in Central America, Oceania and polar regions (Figure 2) (note that these do not
282 include taxa at coarser groupings than species level).

283 The Actinopterygii class included 26 invasive alien fish species with reported costs
284 (US\$34.26 billion). The class Cephalasdomorphi, on the other hand, included only one
285 species, the sea lamprey *P. marinus* (US\$1.39 billion in North America) (Table 1). Observed
286 costs listed for the class Osteichthyes (i.e. bony fish; US\$1.42 billion) were deemed diverse,
287 as this cost entry could not be assigned to a lower taxonomic level (see Pimentel et al., 2000
288 for details). Globally, the ruffe *G. cernua* was the costliest species, followed by the topmouth
289 gudgeon *Pseudorasbora parva*, the sea lamprey *P. marinus*, the common carp *Cyprinus*
290 *carpio*, the red lionfish *Pterois volitans*, unspecific species belonging to *Tilapia* sp., the silver-
291 cheeked toadfish *Lagocephalus sceleratus*, the black bass *Micropterus salmoides*, white bass
292 *Morone chrysops*, the brown trout *Salmo trutta*, and common minnow *Phoxinus phoxinus*
293 (Table 1). All other species contributed less than US\$ 1 million (Table 1).

294 Considering total costs (*potential* and *observed*) inferred in North America, the ruffe
295 *G. cernua* was the costliest species (US\$28.93 billion), followed by *P. marinus* (US\$1.39
296 billion), white bass *M. chrysops* (US\$3.39 million) and brown trout *S. trutta* (US\$1.78
297 million). All other species, such as the northern pike *Esox lucius* and the northern snakehead
298 *Channa argus*, contributed less than US\$1 million.

299 Considering only observed costs globally, *P. marinus* was the costliest species,
300 followed by *C. carpio*, *P. volitans*, *Tilapia* sp., *L. sceleratus*, *M. salmoides*, *M. chrysops*, *S.*

301 *trutta*, and *P. phoxinus* (Table 1). All other species contributed up to US\$1 million (Table 1;
302 Figure 2). Observed costs of *P. marinus*, *S. trutta* and *M. chrysops* were only reported in
303 North America.

304

305 *Cost types and impacted sectors*

306 Costs related to damages and resource losses represented approximately 89% of the observed
307 cost ($n = 96$; Figure 3). Costs associated with management (i.e. control, detection and
308 eradication costs) were an order of magnitude lower, despite having more entries ($n = 196$),
309 while mixed costs amounted to less than US\$1 million ($n = 4$) (Figure 3). In North America,
310 most of the observed cost (US\$1.77 billion) was attributed to damages and losses, with the
311 remaining US\$231.16 million (11.5%) classified as management costs.

312 Considering observed costs, public and social welfare was the most affected sector , followed
313 by costs to fisheries, authorities and stakeholders, the environment and mixed sectors (Figure
314 3). Inferring only observed costs to impacted sectors in North America, the distribution of
315 costs across sectors was similar, with public and social welfare (US\$1.44 billion)
316 predominantly impacted, followed by fisheries (US\$349.81 million), authorities and
317 stakeholders (US\$208.70 million), and mixed sectors (US\$3.27 million).

318

319 *Temporal cost accumulations*

320 In total, costs averaged to US\$607.78 million per year between 1960 and 2020 (Figure 4),
321 with a strong increase from $< \text{US}\$0.01$ million per year in the 1960s to US\$603.08 million per
322 year in the 1980s, before surpassing US\$1 billion by the 2010s. Observed costs averaged to
323 US\$37.43 million per year between 1960 and 2020. Annual observed costs first increased
324 from $< \text{US}\$0.01$ million in the 1960s to US\$159.96 million per year in the 2000s, then
325 decreased after 2010 to US\$7.27 million per year. It should be noted, however, that time lags

326 (i.e. between the occurrence of costs and official reporting) were not accounted for in the last
327 decade (2010 – 2020), and thus cost estimates are therefore likely to be more underestimated
328 in recent years.

329

330 *Comparisons across biotic groups*

331 Records for alien fishes from the IUCN Red List database ($n = 147$, hereafter the number of
332 species) were 30% fewer than recorded alien birds ($n = 210$) and 39% more than recorded
333 alien mammals ($n = 106$). Conversely, fishes were the taxonomic group with the highest
334 number of scientific publications on alien species (17,864 papers), about twice the number of
335 publications on birds (8,759) and four times the number on mammals (4,880) (Figure 5).
336 Nevertheless, invasive alien fish species had the lowest number of unique references reporting
337 costs in the InvaCost database (55) compared to mammals (378) and birds (64). In turn, the
338 total cost of invasive alien fish species (US\$37.08 billion) was much lower than that of
339 mammals (US\$ 424.56 billion), but higher than that of birds (US\$7.52 billion). The
340 distribution of values for each biotic group thus differed significantly (fish vs. birds: $\chi^2 =$
341 2738, $df = 3$, $p < 0.001$; fish vs. mammals: $\chi^2 = 100,000$, $df = 3$, $p < 0.001$; Figure 5), with
342 costs and inputs for fish disproportionately lower than expected based on the number of
343 studies and alien species.

344

345 **Discussion**

346 The total economic cost of invasive alien fishes was US\$37.08 billion globally, from just 27
347 species with reported cost data. These costs are the result of reported/published estimates only
348 which, because of the lack of reported costs in several regions (i.e. Africa and South America)
349 and for several species, suggest that the overall cost estimate is significantly underestimated
350 compared to the actual costs.

351 The reported observed costs are, in fact, very few and are mainly based on damages and
352 resource losses to fisheries, as well as on the costs of large-scale management interventions.
353 For example, the cost of the Eurasian ruffe invasion (*G. cernua*), which accounts for a
354 significant portion of the total cost of invasive alien fish in North America, was extrapolated
355 from population density estimates in Lake Superior to the types of impacts it could have if it
356 were to spread more widely in the Great Lakes basin, resulting in economic costs (potentially
357 reaching US\$500 million by 2050) by impacting recreational fisheries and causing a decline
358 in yellow perch (*Perca flavescens*) populations. This resulted in an estimate of US\$13.6
359 million for a two-year control program and US\$119 million to US\$1.05 billion in benefits
360 from control programmes for recreational and commercial fisheries over a 50-year time
361 period (Lovell et al., 2006). However, because these estimated economic costs have not yet
362 been confirmed, the limited information available on the socio-economic impacts of *G.*
363 *cernua* in the Great Lakes precludes an adequate assessment of economic cost. Nevertheless,
364 it is possible that these potential costs were not overestimated, but rather that the expected
365 impact was mitigated by management, suggesting that the extrapolation may have been robust
366 (and useful) at the time it was made. Other harmful invasive alien fish, such as Asian carp
367 species in the Mississippi River basin, have no current cost estimates, despite the expectation
368 of potential future economic and ecological costs large enough to require the expenditure of
369 US\$831 million to try to prevent spread in the Great Lakes (USACE, 2018).

370 We also showed that the costs of invasive alien fish were significantly lower compared to
371 birds and mammals and the research effort devoted to them. This could be due to a perception
372 bias where damage to habitats or aquatic communities goes unnoticed by the public and
373 authorities because of the difficulties in timely detecting fish invasions compared to other
374 taxa. At the same time, the introduction of aquatic species has often been seen as beneficial to
375 some local communities, especially those engaged in harvesting, processing or recreational
376 tourism (Selge et al., 2011), which leads to a risk of ignoring the negative impacts of the

377 invasion. Invasive alien fish have diverse impacts on ecosystems and understanding their
378 indirect effects will benefit from advances in non-market valuation methods to infer the full
379 range of their impacts (e.g. decline of native species, displacement, extinctions, disease, etc.)
380 (Hanley and Roberts, 2019). Compared to mammals and birds, fish invasions and their
381 vectors of introduction are well studied, with a high number of publications in the natural
382 sciences and reports on the number of invasive alien species (Semmens et al., 2004;
383 Castellanos-Galindo et al., 2020). The low number of reported costs for fish invasions, despite
384 this wealth of literature documenting their presence, likely reflects the difficulties in
385 quantifying their costs and possibly in some cases the fact that certain fish have a long history
386 of intentional introductions (Gozlan, 2008).

387

388 *Taxonomic, regional and environmental biases*

389 In total, economic costs were available for only 27 out of the more than 147 invasive alien
390 fish species worldwide (IUCN, 204 according to FishBase (Froese and Pauly, 2019), with
391 some highly invasive and impactful fish species being completely absent. For example,
392 observed costs have not been reported for the Chinese or Amur sleeper (*P. glenii*) in Europe,
393 although it is a known vector of parasites (Reshetnikov & Sokolov, 2011; Kvach et al., 2013)
394 which may have an important impact on the aquaculture sector (Ondračková et al., 2012).

395 Documented costs of invasive alien fish species also show marked regional disparities, with
396 the majority of reported costs attributed to North America and significantly lower costs
397 reported elsewhere. These regional disparities are not only reflected in the massive differences
398 in costs, but also in the spatial scale of their reporting; a higher proportion of costs in North
399 America were reported at the national level (89 %) compared to costs at the regional (1 %) or
400 local level (10%). These large-scale estimates likely increase the magnitude of reported costs
401 and underscore the need for large-scale estimates outside North America. Despite the fact that
402 a number of fish species have been intentionally introduced to meet the rapidly increasing

403 demand for farmed fish (Lin et al., 2015; Xiong et al., 2015; Grosholz et al., 2015; Zhao et al.,
404 2015; Gozlan 2016), costs of only five invasive alien fish species have been reported in Asia.
405 This is amidst evidence that multiple introduced fish species escape from aquaculture
406 facilities or are released into the wild (Marchetti et al., 2004; Saba et al., 2021). Similarly, the
407 total lack of reporting on the costs of fish invasions in South America and Africa is surprising
408 given the multiple high-profile examples of fish invasions on these continents. For example,
409 in parts of South America (e.g. northern Bolivia), the introduction of *Arapaima gigas* has had
410 serious environmental impacts and is aggressively replacing commercially valuable native
411 fisheries (although *A. gigas* is also fished commercially) (Miranda-Chumacero et al., 2012;
412 Liu et al., 2017; Ju et al., 2019). In East Africa, although the introduction of Nile perch has
413 increased commercial fishing yields, stimulated fish processing and generated income from
414 recreational tourism, it has also had negative effects on local communities by displacing
415 small-scale fishermen and increasing food insecurity and health problems around Lake
416 Victoria (Abila, 2000; Yongo et al., 2005; Aloo et al., 2017). The invasion has also altered the
417 ecological community composition and food web of the lake (Witte et al., 2013), reducing
418 water quality and causing the extinction of around 200 native species (many of them
419 endemic), resulting in one of the largest anthropogenic ecosystem changes ever recorded
420 (Ligtvoet et al., 1991; Kaufman, 1992; Mugidde et al., 2005).

421 With respect to the large difference in costs between North America and Europe, one possible
422 contributing factor worth considering is that the fauna of the Western Palearctic is depleted
423 due to glaciations (Oberdorff et al., 1997). While Nearctic fish faunas were less impacted by
424 glaciations and remained relatively diverse, most fish species in European rivers were
425 intentionally introduced or colonized as a result of anthropogenic activities e.g., the Danube
426 (Levêque et al., 2007). Therefore, invasions in Europe might have an impact, at best, on a
427 limited number of freshwater fishes (or might even have been economically beneficial
428 historically), whereas invasions in North America would necessarily have an impact on a

429 larger number of native species (Levêque et al., 2007). Therefore, compared to other regions,
430 higher costs may also result from the economic importance of the respective freshwater
431 fisheries, which are much more developed in North America than in Europe (e.g. especially
432 for recreational activities such as angling and boating; Franklin, 1998; Mordue 2009).
433 Another potential bias may exist with respect to the regional variation in the number of
434 researchers and institutions studying the impacts of invasive alien fish. That is, that a
435 disproportionately large number of North American researchers may be studying invasive
436 alien fish. This may explain the relatively large investment in management efforts in North
437 America (e.g. for sea lampreys; Stewart et al., 2003; Twohey et al., 2003). Nevertheless, the
438 discrepancies in invasive alien fish costs between North America and Europe cannot be fully
439 explained by differences in economic activity or severity of impacts triggered by invasions. It
440 is also often unclear whether management of invasive populations is driven by ecological or
441 economic rationale between these regions or elsewhere, and InvaCost does not record this
442 information.

443 In contrast to freshwater fish invasions, very few costs are associated with invasive alien
444 marine fish species (Anton et al., 2019, 2020). This is notable given their well-known impacts
445 on marine ecosystems (i.e. on habitat or other native species via competition for food) and on
446 spatially-overlapping commercial fisheries for native species (i.e. costs incurred by bycatch,
447 gear damage, injury, increased fuel consumption to reach invasive-free areas, etc.). Key
448 examples include the angelfish *Pomacanthus* sp. (Semmens et al., 2004), the round herring
449 *Etrumeus golanii* (Galil et al., 2019), the rabbitfish *Siganus rivulatus* and *S. luridus*, the
450 pufferfish *L. sceleratus* in the Mediterranean (Kalogirou et al., 2013; Giakoumi, 2014) and the
451 lionfish *P. miles* (Moonsammy et al., 2011). We think that the low number of entries in the
452 database for marine fish, and for fishes in general, reflect limited knowledge of the costs
453 being incurred, rather than their absence.

454

455 *Conservative nature of reported costs*

456 Considering the biases described above, the cost estimates presented here are likely to be very
457 conservative, as cost data are scarce for most invasive alien fish species and for most regions
458 of the world (see also Diagne et al., 2021 for an overview of the reasons for cost
459 underestimation). A limited understanding of the costs of invasive alien fish is likely to
460 hamper effective communication, investments in detection, control, prevention and
461 management, and relegate them to the bottom of the priority list of policy makers and/or
462 resource managers facing budgetary constraints. This is despite the fact that much of the
463 funding used to manage invasive alien fish in North America comes directly from angling
464 licence sales and taxes on fishing gear and boat fuel, and was therefore not reported or tracked
465 in InvaCost. For example, in 2011, anglers in freshwater ecosystems in the US generated
466 more than US\$40 billion in retail sales, with an estimated total economic impact of US\$115
467 billion and more than 800,000 jobs (Hughes, 2015). Although not reflected in our results for
468 the costs of invasive marine fish, the expenditure of marine anglers is also substantial (\$31
469 billion in 2012), as is the economic impact (US\$82 billion and 500,000 jobs in 2012)
470 (Hughes, 2015). Of course, most of these species are not invasive, but since some of them are,
471 it contributes to the difficulty of comparing costs and benefits of invasive alien fishes.

472 In addition, many of the costs associated with research activities seeking to advance
473 knowledge of invasive alien fish, controlling their populations and mitigating their impacts
474 are generally unreported or inaccessible in the public domain, resulting in an underestimation
475 of investment in relevant research. This is an important driver of limitations inherent in the
476 InvaCost database. Firstly, the monetary costs recorded in InvaCost were largely based on a
477 systematic use of research terms (Diagne et al., 2020a), however, different studies and parties
478 use different terminology to describe invasive alien species. As a result, costs may have been
479 missed in these searches given the pervasive differences in keywords across cost reporting
480 documents. Another similar reason is the fact that some source documents may use the

481 vernacular names that were not considered in the search strings. Additionally, despite the
482 effort to include literature in multiple languages (15 additional non-English languages in
483 InvaCost searches, see Angulo et al., 2021), it has not been possible to cover all languages
484 that may be reporting costs for invasive alien fish globally. This may have exacerbated
485 perceived knowledge gaps in Asia and Africa in particular for which the linguistic coverage
486 was limited. InvaCost is further limited in that only impacts that can be readily monetised are
487 included, resulting in the omission of potential impacts assessed via other measures and
488 metrics, or that are non-market in nature. Furthermore, the methods used to quantify these
489 impacts differ considerably among studies — and although InvaCost uses an objective binary
490 classification for reliability and implementation of the method as a standardised repository for
491 reported costs — it has not been possible to fully account for the variable methodological
492 nature of the underlying studies. The costs in InvaCost therefore directly reflect those reported
493 in the underlying studies, and are subject to their respective potential criticisms. It is
494 important to stress that many of these aforementioned limitations likely make our results
495 substantial underestimates. Considering that InvaCost is a living database meant to be updated
496 on an ongoing basis by authors and future users (Diagne et al., 2020a), we expect that these
497 limitations can be alleviated in the future, yielding improved and more realistic estimates of
498 costs for invasive alien fish and other species.

499 Finally, we note that invasive alien fish species are also known to have economic benefits
500 (especially when they have commercial value) as well as aesthetic and spiritual values
501 (Gozlan, 2010), which requires a better understanding of the trade-offs and incentives to
502 introduce new species and/or maintain a long-term sustainable stock of their invasive
503 population. Considering the benefits of invasive alien fish and understanding these trade-offs
504 was beyond the scope of both the InvaCost database and this paper. However it is an
505 important dimension of managing these species for the greater public good, and one that
506 deserves further exploration in future research. Nevertheless, a comprehensive understanding

507 of the costs and benefits of invasive alien fish is difficult because fish often disperse freely
508 across international borders in seas and rivers, and trade pathways differ greatly between
509 neighbouring countries, while neither costs nor benefits are equally shared.

510

511 **Conclusion**

512 Our work highlights the known and unknown economic costs of invasive alien fish species on
513 a global as well as regional scale. A better understanding of the costs of invasive alien fish
514 species should contribute, for example, to more responsible aquaculture practices, increased
515 awareness of the risk of recreational introductions, and more effective regulatory instruments
516 to prevent accidental species introductions. While it is difficult to predict how the cost of
517 invasive alien fish will evolve worldwide, it is certain that the numbers of introductions of
518 invasive alien species will continue to increase over time (Seebens et al., 2017, 2020). There
519 is accordingly an urgent need to develop more effective and proactive management strategies
520 to prevent fish invasions and promote mitigation of their impacts.

521

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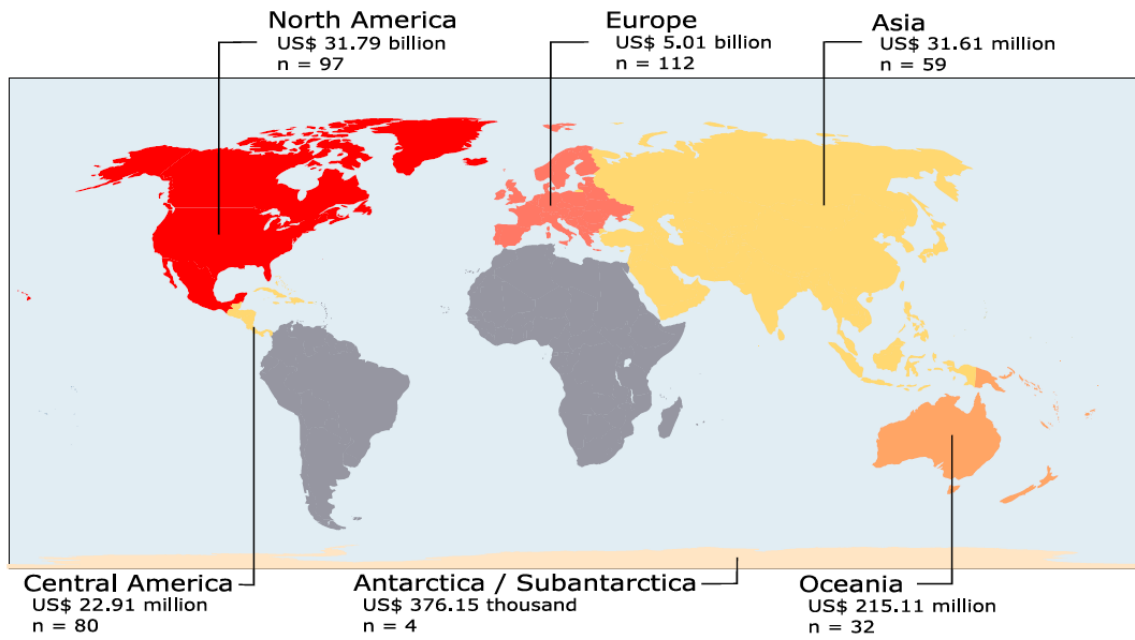
755 **Table 1.** Cost-contributing invasive fish species for total and observed costs, illustrating species, total costs and
756 numbers of database entries; F = Freshwater, M = Marine, B=Brackish (according to the environment
757 classification of Froese and Pauly, 2019).

Common name	Genus	Species	Environment	Total costs		Observed costs	
				Cost (US\$ 2017 value) in million	database entries	Cost (US\$ 2017 value) in million	database entries
Brown bullhead	<i>Ameiurus</i>	<i>nebulosus</i>	F	0.001	3	0.001	3
Goldfish	<i>Carassius</i>	<i>auratus</i>	F,B	0.001	3	0.0010	3
Northern snakehead	<i>Channa</i>	<i>argus</i>	F	0.138	1	0.138	1
Redbelly tilapia	<i>Coptodon</i>	<i>zillii</i>	F,B	0.011	3	0.011	3
Common carp	<i>Cyprinus</i>	<i>carpio</i>	F,B	216.978	48	216.773	28
Northern pike	<i>Esox</i>	<i>lucius</i>	F,B	0.021	1	-	-
Mummichog	<i>Fundulus</i>	<i>heteroclitus</i>	M,F,B	0.017	5	0.017	5
Eastern mosquitofish	<i>Gambusia</i>	<i>holbrooki</i>	F,B	0.009	10	0.009	10
Ruffe	<i>Gymnocephalus</i>	<i>cernua</i>	F,B	28,933.217	47	-	-
Silver-cheeked toadfish	<i>Lagocephalus</i>	<i>sceleratus</i>	M	6.540	15	6.247	13
Pumpkinseed	<i>Lepomis</i>	<i>gibbosus</i>	F,B	0.030	13	0.030	13
Bluegill	<i>Lepomis</i>	<i>macrochirus</i>	F	0.073	10	0.073	10
Black bass	<i>Micropterus</i>	<i>salmoides</i>	F	5.293	34	5.293	34
White bass	<i>Morone</i>	<i>chrysops</i>	F	3.394	1	3.394	1
Rainbow trout	<i>Oncorhynchus</i>	<i>mykiss</i>	M,F,B	0.016	2	0.016	2
European perch	<i>Perca</i>	<i>fluviatilis</i>	F,B	0.014	3	0.014	3

Chinese sleeper	<i>Percottus</i>	<i>glenii</i>	F,B	0.173	4	-	-
Sea lamprey	<i>Petromyzon</i>	<i>marinus</i>	M, F, B	1,389.395	15	534.887	12
Common minnow	<i>Phoxinus</i>	<i>phoxinus</i>	F,B	1.210	3	1.210	3
Guppy	<i>Poecilia</i>	<i>reticulata</i>	F	0.017	2	0.017	2
Topmouth gudgeon	<i>Pseudorasbora</i>	<i>parva</i>	F,B	5,004.319	22	0.818	11
Red lionfish	<i>Pterois</i>	<i>volitans</i>	M	24.528	85	24.528	85
Janitor fish	<i>Pterygoplichthys</i>	sp.	F	0.002	1	0.002	1
Brown trout	<i>Salmo</i>	<i>trutta</i>	M,F,B	1.782	10	1.782	10
Zander	<i>Sander</i>	<i>luciperca</i>	F,B	0.022	4	0.022	4
European catfish	<i>Silurus</i>	<i>glanis</i>	F,B	0.002	1	0.002	1
Tilapia	<i>Tilapia</i>	sp.	F	20.039	1	20.039	1
		Diverse/unspecified		1,467.556	31	1,467.556	31

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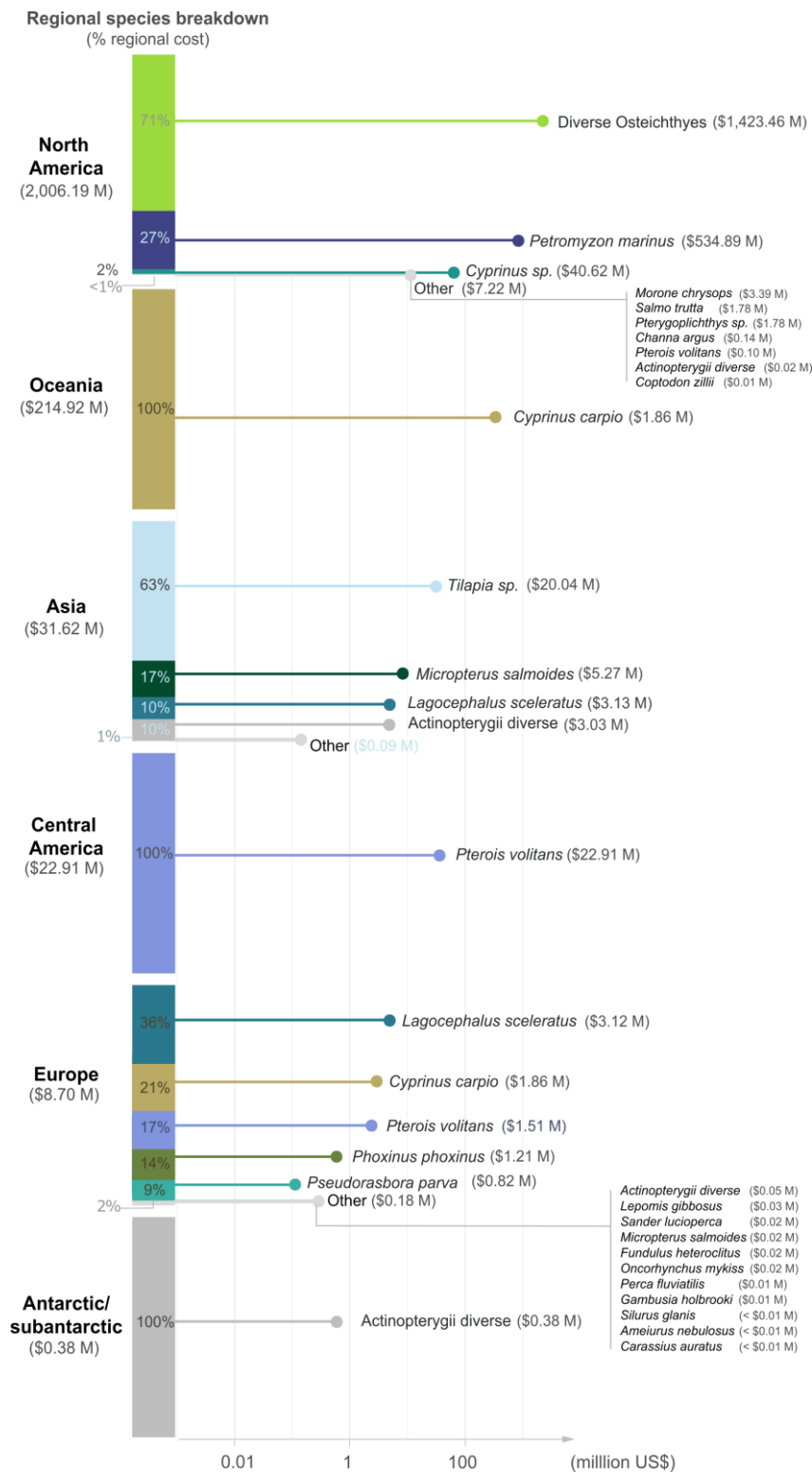
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761 **Figure 1.** Total costs (observed and potential) of invasive fishes by geographical region. Grey

762 indicates no cost information being available for that region, yellow to red indicates the magnitude of

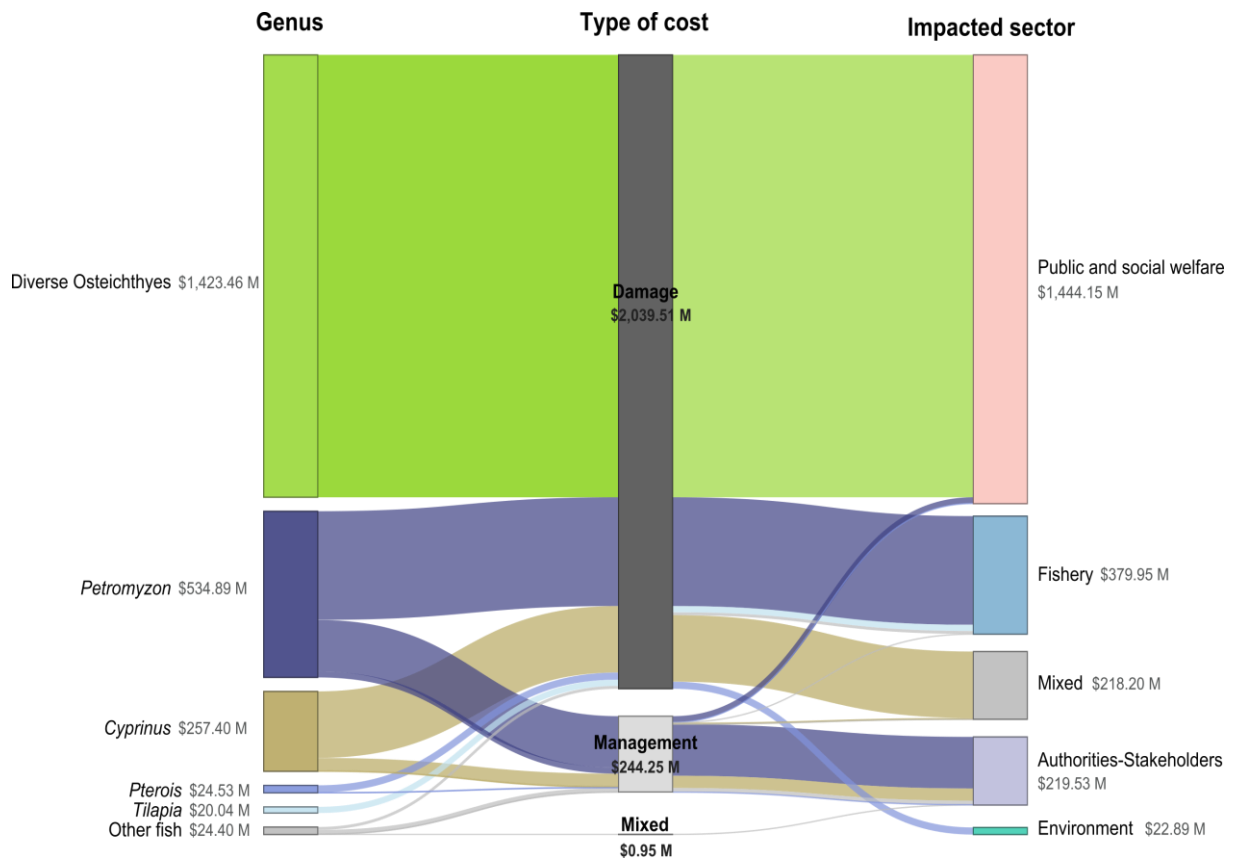
763 the reported costs.

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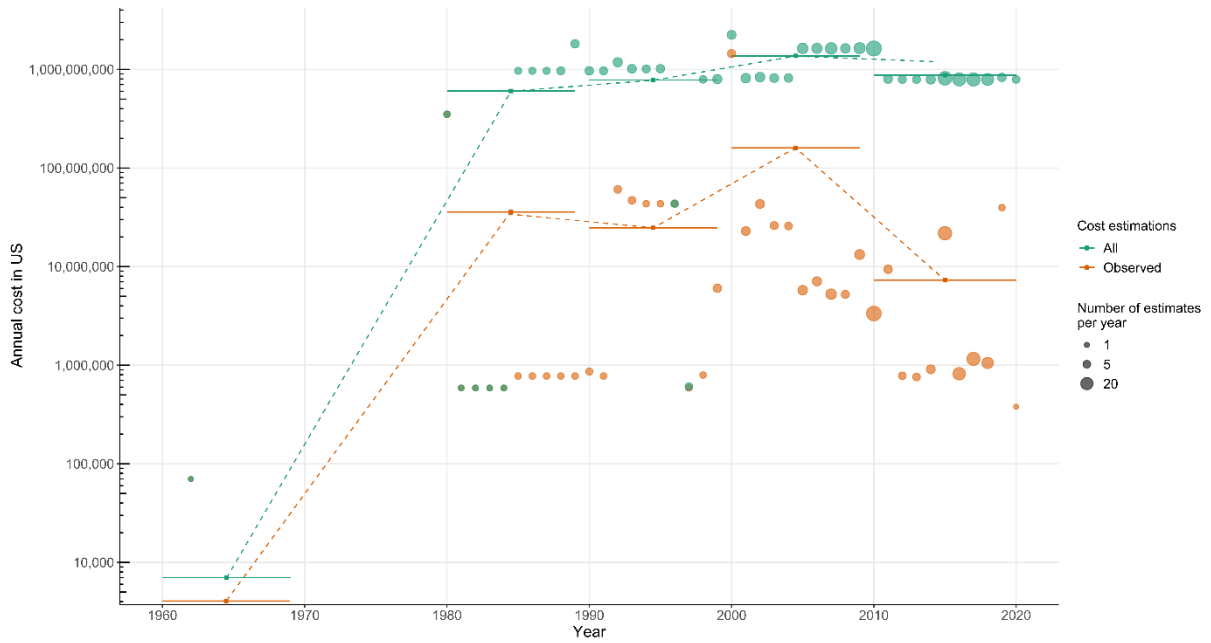
766 **Figure 2.** Observed costs of invasive fish species across regions (North America, Europe, Asia,
 767 Antarctic/Sub-Antarctic and Central America) indicating the contribution of the species to the
 768 respective total. For example, *Pterois volitans* accounts for 100% of the costs of invasive fish in
 769 Central America and contributes US\$0.02 million to the total cost of invasive species. Note that the *x*-
 770 axis is on a log₁₀ scale.



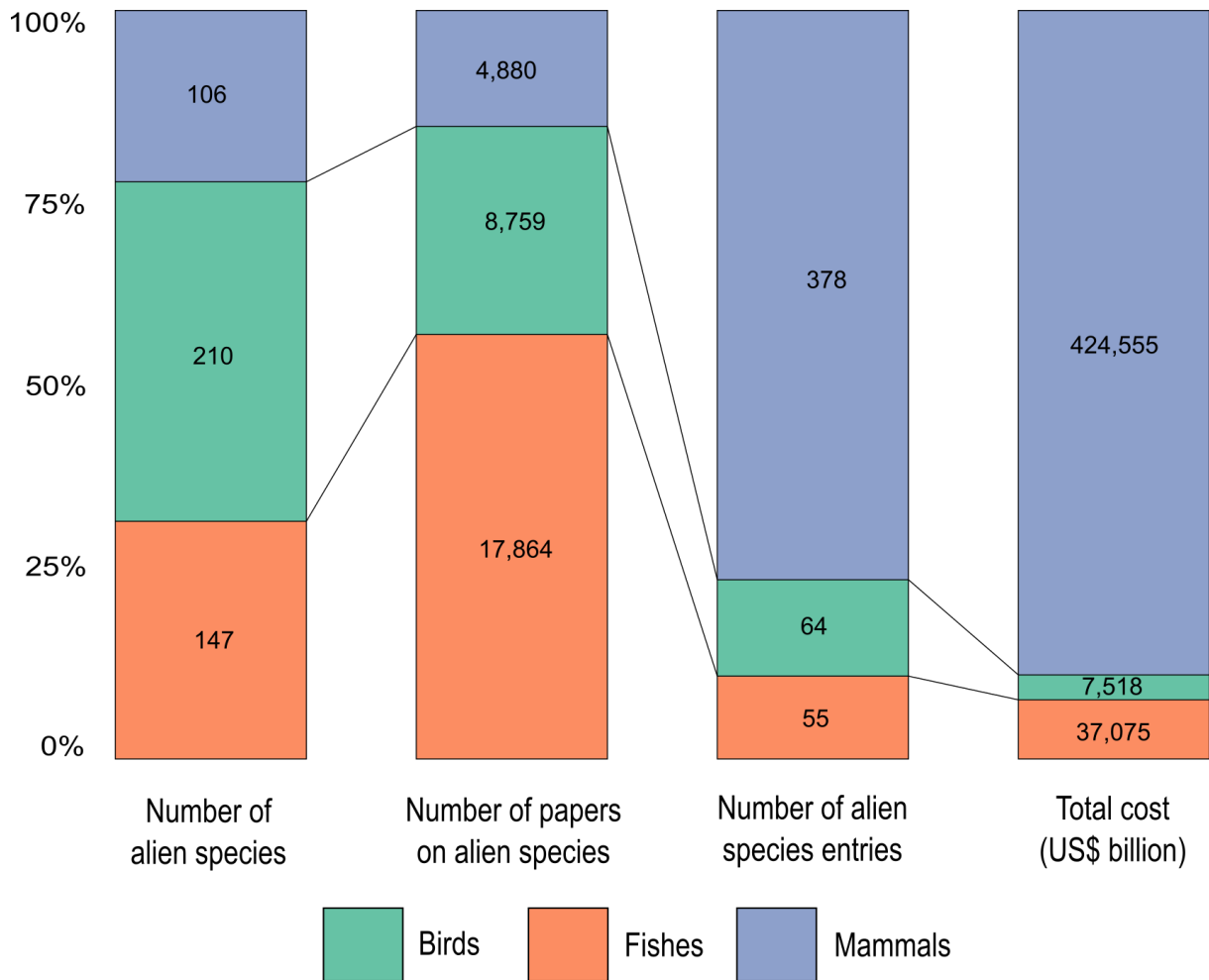
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772 **Figure 3.** Sankey diagram showing the distribution of observed costs of alien fish invasions across
 773 genera, types of costs and sectors affected. Costs are shown in millions of US 2017 dollars.

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 776 **Figure 4.** Total (green) and observed (orange) average annual costs in billions of 2017 US\$ resulting
 777 from global invasions by fish. Points are annual values scaled by the number of annual estimates. Note
 778 that the y-axis is represented on a log₁₀ scale.
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Figure 5. Comparison among fishes, birds and mammals based on the numbers of alien species,

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numbers of articles on alien species, entries and costs in the InvaCost database.