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Research Article

Impacts of non-native fishes: from global patterns to Indian contexts

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Abstract

Impacts of non-native fish species (NNF) on ecosystems and human communities can be substantial and in principle be either detrimental or beneficial for native species or people. Studies on NNF vary geographically, with little research comparing NNF impacts in wealthier countries to those in other parts of the world. We assessed impacts of the 20 most widely distributed fish species that are non-native to India and compared their documented impacts in India with those elsewhere in the world. We considered detrimental and beneficial environmental and socio-economic impacts, applying all four Impact Classification for Alien Taxa (ICAT) tools to assess impacts of non-native species: the IUCN Environmental Impact Classification for Alien Taxa (EICAT), EICAT+, Socio-Economic Impact Classification for Alien Taxa (SEICAT), and SEICAT+. Five NNF were classified as Data Deficient due to a lack of relevant impact records. Among the 442 relevant impact records for the 15 remaining NNF at the global scale, detrimental environmental impacts dominated (384), with fewer records pertaining to beneficial environmental (34), detrimental socio-economic (14) and beneficial socio-economic (10) impacts. A predominance of detrimental environmental impacts (35) over all other impact types (10) was also detected for India. Our results show that NNF can cause reductions in the population size of native species, particularly in macrophytes. Severity of detrimental environmental impacts (at the individual or population level of native taxa) did neither vary with transfer type (inter- or intra-realm), nor impact location (India or rest of the world), nor detection type (observed, field experiment, in-situ mesocosm, exclosure/enclosure experiment, or intervention). Based on our findings, we suggest prioritizing macrophytes for threat evaluation—while emphasizing that other taxa are not free from risk from NNF—and conducting targeted studies in India to detect impacts of NNF and fill critical impact data gaps.

Key words: EICAT, freshwater fishes, ICAT framework, impact assessment, invasive alien species, SEICAT

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Introduction

Fish species moved intentionally or unintentionally by human activities beyond the limits of their native geographic range, or resulting from breeding or hybridisation and escaping or being released into an area where they do not naturally occur, are known as non-native fishes (NNF) (IUCN 2020). The human-mediated movement and establishment of NNF has been documented worldwide (Bernery et al. 2022), and caused various environmental and socio-economic impacts, affecting both biodiversity and human well-being. While these impacts can be either

detrimental or beneficial (Vilà et al. 2010; Vimercati et al. 2020), a given species can cause diverse impacts simultaneously. For instance, rainbow trout (*Oncorhynchus mykiss*) have caused the local extirpation of endemic fishes in South Africa, a detrimental environmental impact (Shelton et al. 2015). However, they have also increased the abundance of native aquatic insects in the Nyanga National Park, Zimbabwe, a beneficial environmental impact (Kadye et al. 2013). Furthermore, fishery of introduced rainbow trout has been established as a novel activity in the Colorado River, USA, providing socio-cultural benefits and generating economic value, a beneficial socio-economic impact (Bair et al. 2016). Detrimental socio-economic impacts have been caused by bighead and silver carp (*Hypophthalmichthys nobilis* and *H. molitrix*) through their jumping behaviour, which threatened the safety of recreational fishers, swimmers and boaters in the Illinois river, USA (Spacapan et al. 2016).

India has a history of freshwater fish introductions dating back to the mid-19th century, and some of the 58 NNF currently detected in the wild (Kumar et al. 2025) have been linked to measurable impacts. For instance, brown trout (*Salmo trutta*) have been reported to displace populations of native snow trout (*Schizothorax richardsonii*) in the Indian Himalayan rivers (Sharma et al. 2021). Similarly, adverse impacts of Mozambique tilapia (*Oreochromis mossambicus*), Nile tilapia (*O. niloticus*) and African catfish (*Clarias gariepinus*) on native taxa through predation and grazing have been documented (Singh et al. 2012; Raj et al. 2021; Roshni et al. 2021). Additionally, a few studies have detected beneficial impacts of NNF on local human communities in India, such as increased income and employment, and reduced occurrences of vector-borne diseases, for example Chikungunya (Johnson et al. 2020; Singh et al. 2022). However, research into invasion biology is more often conducted in wealthier regions such as North America, Europe and Australia (Olden et al. 2008; Bellard et al. 2016; Bernery et al. 2022), while e.g. India has had fewer research activities on biological invasions. Furthermore, only about 19% (62 of 332 reports) of studies included in a systematic review of NNF in India attempted to document their impacts (Kumar et al. 2025), compared with 32% of studies in a global review of all non-native species (Lowry et al. 2013). Therefore, assuming that impacts of NNF in India have been understudied, but also that India is similarly impacted by NNF invasions as the Rest of the World (RoW), we hypothesize that the probability of detecting strong impacts in India is lower, reflecting limitations in research effort rather than genuinely weaker impacts (hypothesis 1).

Detection of environmental impacts of NNF impacts is influenced by the methodological approach (observational or manipulative) used in a study (Parker et al. 1999; Kumschick et al. 2015). Závorka et al. (2018) found that manipulative studies reported significantly stronger negative environmental impacts of non-native brown trout than observational studies. However, manipulative study designs (experiments) can range from simple laboratory experiments, such as observing comparative predation of native and non-native fishes on ringed salamander eggs and larvae in laboratory glass tanks (Drake et al. 2014), to complex interventional experiments in natural ecosystems, such as removing invasive common carp from lakes and investigating the consequences with before after invasion surveys (Maceda-Veiga et al. 2017). Volery et al. (2020) suggested that in experimental studies, population-level impacts of NNF can be observed only when the experiments are conducted on native populations that are self-sustaining. In addition, a recent study reinforces the view that complex experiments involving multiple species interactions are better at capturing environmental

impacts compared to single-species experiments (Jakubavičiūtė et al. 2025). The ability to infer impacts from an experimental study depends on the type of experimental setup and how closely it replicates natural ecosystem conditions. Moreover, experiments in natural ecosystems (for example, before-after invasion surveys) require a significantly higher investment compared to laboratory experiments (Christie et al. 2019). In the present study, we categorised manipulative study designs based on how close they are to natural conditions (see Methods section for details) and tested which methodological approaches (observational versus different manipulative study types) are more likely to detect stronger environmental impacts. We therefore hypothesised that manipulative studies closer to natural conditions will report stronger environmental impacts than other studies (hypothesis 2). Additionally, given the financial demands of conducting experiments within natural ecosystems and India's classification as a member of the Global South, we hypothesized that observational studies will be predominant in India compared to the RoW (hypothesis 3).

Environmental impacts of NNF are influenced by the evolutionary history of NNF and their interactions with the native communities (Ricciardi and Atkinson 2004; Saul and Jeschke 2015; Britton 2023). The concept of environmental naivety posits that the impact of non-native species is influenced by the eco-evolutionary experience of native species, with more severe impacts expected from non-native species that are phylogenetically or functionally distinct from native species compared to those that are similar (Diamond and Case 1986; Ricciardi and Atkinson 2004; Enders et al. 2020). In support of this, Ricciardi and Atkinson (2004) found that aquatic non-native species from genera not represented in the local fauna caused high impacts (i.e., promoting > 80% decline in the population of one or more native species). Accordingly, we hypothesised that introductions across biogeographic realms (inter-realm transfers) cause stronger detrimental environmental impacts than those within the same realms (intra-realm transfers) (hypothesis 4). This is because species from different realms are likely to be more distinct from the native communities, hence the native species will have limited eco-evolutionary experience. With respect to impacts on different taxonomic groups, a global meta-analysis showed that aquatic non-native species, particularly those that have omnivorous and herbivorous feeding strategies, reduce the abundance of native aquatic species, with native macrophytes experiencing the greatest declines (Gallardo et al. 2016). Similarly, impacts of NNF were reviewed by Britton (2023), who reported that NNF reduce macrophyte biomass through herbivory and physical disturbance. Thus, assuming that macrophytes are more vulnerable than vertebrates or invertebrates, we hypothesize that they experience stronger detrimental impacts than these animal groups (hypothesis 5).

Among the various tools available to score impacts of non-native species (see e.g., González-Moreno et al. 2019), the Impact Classification for Alien Taxa (ICAT) framework offers an evidence-based and transparent approach to assess both detrimental and beneficial environmental and socio-economic impacts. Specifically, the Environmental Impact Classification for Alien Taxa (EICAT) is an IUCN (International Union for Conservation of Nature) standard used to assess detrimental environmental impacts (Blackburn et al. 2014; IUCN 2020). EICAT+ focuses on beneficial environmental impacts (Vimercati et al. 2022), while the Socio-Economic Impact Classification for Alien Taxa (SEICAT) assesses detrimental socio-economic impacts (Bacher et al. 2018; Probert et al. 2023), and SEICAT+ focuses on beneficial socio-economic impacts (Vimercati et al. 2025).

These tools offer the opportunity to compare impacts across taxa, habitats and regions (Blackburn et al. 2014). Earlier research has used the ICAT framework to assess impacts of various taxa, including fishes. Specifically, Chen et al. (2024) employed EICAT and EICAT+ for freshwater megafish species, and Chen et al. (2026) employed SEICAT together with other approaches for freshwater megafauna. Additionally, EICAT, in combination with other tools, was used to classify the impacts of channel catfish (*Ictalurus punctatus*) in Italy (Haubrock et al. 2021) and ruffe (*Gymnocephalus cernua*) in Turkey (Tarkan et al. 2022). Similarly, detrimental environmental and socio-economic impacts of seven high-risk marine fishes were evaluated using EICAT and SEICAT (Galanidi et al. 2018). However, to the best of our knowledge, no study has so far used the complete ICAT framework consisting of all four tools to assess the impacts of any taxonomic group.

In the present study, we globally assessed both the detrimental and beneficial environmental and socio-economic impacts for the 20 most widely distributed fish species that are non-native to India (cf. Kumar et al. 2025). In general, we report on data availability across different impact types, impact magnitudes and geographic regions, and summarize species associated with the highest number of impacts. We identify: the most impactful NNF by using the four ICAT tools; the most impacted native biological group (macrophytes, vertebrates and invertebrates), and dominant mechanisms through which NNF have caused detrimental and beneficial impacts on native biological groups by using EICAT and EICAT+); the type of human communities (groups of people following similar activities) that experienced detrimental and beneficial impacts of NNF as well as the impacted constituents of human well-being (i.e., the ways in which these human communities were impacted) by using SEICAT and SEICAT+. Additionally, we map the distribution of impact records across biogeographic realms and identify the realm with the highest number of records. Furthermore, we aim to test the hypotheses that: (1) the probability of detecting strong detrimental environmental impacts in India is lower compared to the RoW, (2) manipulative studies closer to natural conditions report stronger environmental impacts than other studies, (3) observational studies are predominant in India compared to the RoW, (4) inter-realm transfers cause stronger detrimental environmental impacts than intra-realm transfers, and (5) aquatic macrophytes experience stronger detrimental impacts than animal groups.

Methods

Species assessed

Kumar et al. (2025) mapped the spatial distribution of NNF in India of which we selected the 20 most widely distributed NNF for the assessment. Impacts of these 20 NNF in their introduced range were assessed in India, and at the global scale (Table 1).

Data

We searched in two online databases, Web of Science and Google Scholar, to retrieve relevant reports for the assessment. To identify reports for assessments at the global level, the search string [("invasive" OR "exotic" OR "alien" OR "introduced" OR "non-native" OR "nonnative" OR "non-indigenous" OR "nonindigenous" OR "IAS") AND ("impact" OR "effect" OR "affect" OR "influence")

Table 1. The 20 most widely distributed NNF in India that were assessed in this study, their presence in number of river basins in India (based on Kumar et al. 2025) and their maximum ICAT score at the global scale (results from this study). Species with an asterisk (n = 5) are those for which no relevant impacts were recorded based on the available literature and therefore assessed as DD.

Family	Species	# basins	EICAT	EICAT+	SEICAT	SEICAT+
Lepisosteidae	*Atractosteus spatula**	3	DD	DD	DD	DD
Salmonidae	*Oncorhynchus mykiss*	4	MR	MO+	DD	MR+
	Salmo trutta	3	MV	MO+	DD	MO+
Cyprinidae	*Barbonymus gonionotus*	4	MN	DD	DD	DD
	Carassius auratus	4	MR	DD	DD	DD
	Ctenopharyngodon idella	11	MR	MO+	DD	DD
	Cyprinus carpio	12	MR	MO+	DD	MN+
Xenocyprididae	*Hypophthalmichthys molitrix*	10	MR	MO+	MO	DD
	Hypophthalmichthys nobilis	4	MO	MO+	MO	DD
Clariidae	*Clarias gariepinus*	10	MR	DD	DD	DD
Loricariidae	*Pterygoplichthys disjunctivus*	3	MN	DD	MN	DD
	*Pterygoplichthys pardalis**	5	DD	DD	DD	DD
	*Osphronemus goramy**	4	DD	DD	DD	DD
Pangasiidae	*Pangasianodon hypophthalmus**	7	DD	DD	DD	DD
Serrasalmidae	*Piaractus brachypomus*	5	MN	DD	DD	DD
Poeciliidae	*Gambusia affinis*	10	MO	DD	DD	MN+
	Poecilia reticulata	8	MR	DD	DD	DD
Cichlidae	*Amphilophus trimaculatus**	3	DD	DD	DD	DD
	Oreochromis mossambicus	13	MR	DD	MC	DD
	Oreochromis niloticus	11	MV	MO+	MN	MN+

AND ("[scientific name of the species]" OR "[common name of the species]")] was run on the Web of Science. Kumar et al. (2025) conducted a systematic review of NNF in India using the Web of Science and Google Scholar and reported that 79% of the studies (262 of the 332) were found in Google Scholar primarily due to indexing and the accessibility of alternative record types. Therefore, to search for reports pertinent to India, the modified string [("invasive" OR "exotic" OR "alien" OR "introduced" OR "non-native" OR "nonnative" OR "non-indigenous" OR "nonindigenous" OR "IAS") AND ("impact" OR "effect" OR "affect" OR "influence") AND ("scientific name of the species" OR "common name of the species") AND "India"] was run on Google Scholar. In Google Scholar, only the first 200 reports of the results were evaluated for each NNF because Google Scholar returns a long list of results with decreasing relevance. The reports that contained information on the detrimental and/or beneficial environmental and/or socio-economic impacts, which we assessed based on the title, abstract and content of the record, were considered relevant to the study. We also compared the maximum EICAT and EICAT+ scores with those reported by Chen et al. (2024) for those species that were assessed in this previous study and the current study. For one species (*Salmo trutta*), Chen et al. (2024) assigned a higher EICAT+ score than our initial assessment (see Suppl. material 1: table S1). We reviewed the additional sources they had accessed, which were not retrieved in our literature search (i.e. Flecker and Townsend 1994; Biggs et al. 2000; Nyström and McIntosh 2003; Milardi et al. 2016). Finally and also for overlapping species, we compared the literature used for impact assessment of non-native species in the Global Impact Database of Invasive Alien Species (GIDIAS) (Bacher et al.

2025) with the literature in our study to identify additional relevant reports that were not detected in our search. Such reports were then independently assessed by us and included in our dataset.

Classification of manipulative studies

Several studies employed a manipulative approach to detect the environmental impacts of NNF. In accordance of the suggestions by Probert et al. (2020) on using experimental studies to reduce systematic bias and improve the reliability of EICAT impact scores, we classified manipulative approaches into seven categories: laboratory experiment, ex-situ mesocosm, field experiment, in-situ mesocosm, enclosure experiment, exclosure experiment and intervention. The categories are ordered from artificial towards increasingly natural conditions, with laboratory experiments being farthest and intervention being closest to natural conditions (see Suppl. material 1: tables S2, S3 for a description of these methodological approaches together with examples). Volery et al. (2020) clarified that reporting population-level impacts (MO, MR, MV) in EICAT is only possible when self-sustaining native populations are monitored (ideally across several generations). For non-self-sustaining populations, impacts can only be assessed at the individual performance level (MN). These criteria were considered when classifying the manipulative methods. In addition, we considered the relative size of the impacted taxa in relation to the experimental setup, to determine the maximum possible impact score that could be assigned to each record.

For example, field experiments were often carried out in relatively large human-made earthen waterbodies (ponds) (12 to 400 m^2). Ponds with plastic linings were excluded. Generally, experimental ponds were prepared before the start of the trial by cleaning, drying, and filling with water. Experiments were initiated after the pond had stabilized (sometimes up to five weeks) by adding the focal native and non-native species. Because these earthen ponds had direct contact with soil and were exposed to sunlight, we assumed that they developed natural ecosystem dynamics from the outset. However, because the ponds were prepared before the onset of experiments and the biota were selectively added, we classified them as semi-natural systems. In this setting, when the impact of NNF was assessed on invertebrates such as plankton, we recorded impacts at the population level because plankton establishes self-sustaining populations within the ponds. However, impacts were scored only up to the "moderate" (MO) category, as higher impacts (MR, MV) could not be inferred from such semi-natural systems. In contrast, impacts on vertebrates were recorded only at the individual performance level (MN), because these species do not have a self-sustaining population within the experimental ponds.

Impact assessment

We classified the detrimental and beneficial environmental and socio-economic impacts of NNF using the full ICAT framework. While EICAT and EICAT+ measure environmental impacts of non-native species on native biodiversity as changes at the individual and population level, SEICAT and SEICAT+ measure socio-economic impacts as changes to human activities and well-being. All four tools in the ICAT framework follow a set of criteria that are used to classify observed (not inferred or potential) impacts into five ordinal categories ranging from Minimal

to Massive, known as impact scores (see Suppl. material 1: fig. S1). In this study, a 'report' is a published study that may describe more than one impact observations. Each distinct impact of a NNF on a native taxon (as defined by EICAT and EICAT+) or on a human activity (as defined by SEICAT and SEICAT+) is treated as an 'impact record'. When a report describes impacts on multiple native taxa or human activities, each is counted as a separate impact record. An impact record was assigned as Not Applicable (NA) when an impact was suggested, but the report did not provide sufficient information to determine the level of impact magnitude under ICAT. All NNF for which no impacts were found or for which all impact records were classified as NA were assigned the category Data Deficient (DD) and they were not considered for statistical analysis. For example, we found three reports on *Osphronemus goramy*. Each report discussed only inferred impacts, but no observed impact was described. As a result, all three impact records (derived from three reports) were classified as NA, and the species was classified as DD.

Following the guidelines for ICAT (Bacher et al. 2018; IUCN 2020; Volery et al. 2020; Vimercati et al. 2022, 2025; Probert et al. 2023), the impact score assigned in a record was supplemented with additional information such as impacted location (place, region, country, continent, coordinates) and impacted biogeographic realm. To account for uncertainty in the assigned impact score, each impact score was given a confidence score (low, medium, or high) based on the confidence that the assigned impact score is correct (Probert et al. 2020). The EICAT and EICAT+ impact scores were assigned with one of the pre-defined impacts (sub-)mechanisms, impacted native species (scientific name, common name, order to which they belong) and higher biological level (vertebrate, invertebrate, and macrophytes). The SEICAT and SEICAT+ assessments were supplemented with information on the spatial scale of the impact (local, regional, national or multi-national), type of impacted human communities (group of people following similar activities, e.g. fishers, swimmers), and the ways in which these human communities are impacted i.e., their safety, material and immaterial assets, health, social/cultural/spiritual relations, and freedom of choice and action, which are known as constituents of human well-being (Bacher et al. 2018). SEICAT and SEICAT+ also have provision to document peoples' 'ability to doing' and 'ability to being', where 'doings' refer to activities (e.g. fishing, swimming, or boating) and 'beings' refer to a state a person has achieved (e.g. being healthy or financially stable) (Probert et al. 2023; Vimercati et al. 2025). SEICAT and SEICAT+ have the additional provision to assess 'burdensome activities', which are extra or novel tasks (activities) initiated by the affected people as a response to detrimental impacts of non-native species aimed to reduce such impacts (Probert et al. 2023; Vimercati et al. 2025). For additional information included in the ICAT assessments and assigning impact magnitude, impact mechanisms, the constituent of human well-being impacted, the type of impact, and confidence scores, please refer to Suppl. material 2 and ICAT guidelines (Bacher et al. 2018; IUCN 2020; Vimercati et al. 2022, 2025; Probert et al. 2023).

Data preparation

Leroy et al. (2019) proposed the major biogeographical regions and transition zones for freshwater fish species which we adopted in this study. Both the terrestrial biogeographic realms (Indo-Malaya, Australasia, Neotropic, Afrotropic, Nearctic, and Palearctic) and the freshwater biogeographic regions defined by Leroy et al.

(2019) (Nearctic, Neotropical, Palearctic, Ethiopian, Sino-Oriental and Australian) are continental in scale. Although Leroy et al. (2019) used the term 'biogeographic regions', we refer to these units as 'biogeographic realms' to align with previous studies that used terrestrial biogeographic realms and to keep the terminology consistent across scales. For each assessment, we assigned biogeographic realms corresponding to both native and impacted areas. We created two variables, 'transfer type' (intra or inter-realm) and 'impact location' (India or RoW), with the former indicating if the native range and non-native area where the NNF was studied are within the same biogeographic realm, and the latter indicating if the impacts of the NNF were reported in India or other part of the globe, respectively. Further, the five impact magnitudes were grouped as 'strong' (MO, MR and MV) vs 'weak' (MN and MC) impacts following previous works (Evans et al. 2016; Forgione et al. 2022; Bescond-Michel et al. 2025).

Statistical analyses

As there were few socio-economic impact records in our dataset, statistical analyses were limited to environmental impacts. Analyses were performed in R version 4.3.2 (R Core Team 2023). First, binomial generalized linear mixed-effect models (GLMMs) were built using the package 'lme4' (Bates et al. 2015) to test which variables predict the probability of strong detrimental environmental impacts of NNF using EICAT assessments (n = 384). The response variable was impact magnitude ('strong' as '1', 'weak' as '0'). Fixed effects were impacted groups (macrophytes, invertebrates, vertebrates), impact location (India vs. RoW), and transfer type (intra-realm vs inter-realm). Impacted realm (Australian, Ethiopian, Nearctic, Neotropical, Palearctic and Sino-oriental) and the scientific name of the NNF were included as random effects to account for pseudo-replication resulting from multiple impact observations from same realm and/or same NNF. Models were compared and ranked based on their corrected Akaike Information Criterion (AICc) using the 'MuMIn' package (Barton 2019). The relative importance (sum of Akaike weights; Anderson and Burnham 2002) of the predictors in the best fitting models (ΔAICc < 6; Richards 2008) was estimated to identify the predictors (fixed effects) with adequate explanatory power (>0.5). The evidence ratio ($\omega 1/\omega i$, where $\omega 1$ is the Akaike weight of the best-fitting model) was calculated to assess the probability that each model provides the best fit to the underlying data. Higher ratios are indicative of greater support for the best-fitting model, whereas lower ratios demonstrate comparatively stronger support for alternative models (Bescond-Michel et al. 2025). A model containing only variables that had adequate explanatory power (> 0.5) and evidence ratio (< 2) was considered as the most supported and used for pairwise comparison and graphical representations. To confirm that the selected model met its assumptions, we used the R package DHARMa (Hartig 2024) to check residual normality with a QQ plot and to test for overdispersion (p = 0.8) and outliers (p = 1).

Because only eight of the 15 NNF that were not classified as Data Deficient had impacts documented in both India and the RoW (Suppl. material 1: fig. S2), we built binomial GLMM with impact magnitude as response variable (strong vs. weak), impact location (India vs. RoW) as fixed effect, and impacted realm and scientific name of species as random effects to test whether impacts were more severe in India with this subset of the data (n = 190).

A third group of binomial GLMM was built to test the probability of methodological approaches in reporting strong environmental impacts of NNF. The response variable was impact magnitude (strong vs. weak), the fixed effect was methodological approach (observational studies, field experiments, enclosure experiments, exclosure experiments, and interventions), and impacted realm and scientific name of the NNF were random effects. Laboratory experiments and ex-situ mesocosms were excluded because they were always scored as NA. In-situ mesocosms were also excluded because all 12 assessments reported strong impacts and provided no variance, though including them did not change model results (data not shown). As both detrimental and beneficial environmental impacts were assessed using manipulative studies, the impact records from both EICAT and EICAT+ were combined for this analysis (n = 406). The model showed no evidence of a singular fit and conformed to DHARMa residual tests (overdispersion: p = 0.17, outliers: p = 1).

Significant differences among levels of categorical variables were identified by Tukey's pairwise multiple comparisons using 'emmeans' package (Lenth 2025). Figures were plotted using the package "ggplot2" (Wickham 2016). Lastly, Fisher's exact test was used to determine whether observational studies were more frequent in India than the RoW.

Results

Environmental and socio-economic impacts of NNF varied in both directions (detrimental or beneficial) and between India and the RoW. In total, we derived 1,353 records of which 911 records (67%) were scored as NA, while the remaining 442 records (33%) were scored for an impact between minimal concern (MC) and massive (MV) (Suppl. material 1: fig. S3). Among these 442 impact records, detrimental environmental impacts (EICAT) dominated (n = 384), followed by EICAT+ (n = 34), SEICAT (n = 14) and SEICAT+ (n = 10) (Fig. 1). Of the 418 environmental impact records (EICAT and EICAT+ combined), the majority (304 records) were derived from observational studies, with the remainder (114 records) coming from manipulative studies (Fig. 2). However, a higher proportion of strong impacts (67%, i.e. 77 of 114 records) was observed in the manipulative studies compared to the observational studies (47%, i.e. 145 of 304 records). A total of 45 impact records were from India, with a further 397 originating from the RoW (Fig. 3A). Detrimental environmental impact records dominated globally as well as in India over all other types of impacts (Fig. 3B, C). Although the detrimental environmental impacts and socio-economic impacts were reported from India in varying proportions, no beneficial environmental impacts were reported in the country (Fig. 3C).

Of the 20 NNF assessed, 15 species had reported impacts that were scored from MC to MV, while five species (*Atractosteus spatula, Amphilophus trimaculatus, Osphronemus goramy, Pterygoplichthys pardalis and Pangasianodon hypophthalmus*) were assessed as DD as they had no relevant impact data (Fig. 1). At the global level, 15 species had documented detrimental environmental impacts of which 11 had strong impacts (i.e., reducing population of native taxa or causing reversible/irreversible extirpation). Two NNF, the brown trout (*Salmo trutta*) and Nile tilapia (*Oreochromis niloticus*), were responsible for the extinction of native fish, the New Zealand Greyling, *Prototroctes oxyrhynchus*, and short-barbelled barb, *Labeobarbus microbarbis*, respectively (i.e., massive impact MV), whereas nine NNF were found to have locally extirpated native taxa (MR; Fig. 1). Common carp (*Cyprinus carpio*) had the greatest number of documented

		Environmental Impacts								Socio-economic Impacts					
		EICAT					EICAT+			SEICAT			SEICAT+		
Family	Non-native fish species	MC	MN	MO	MR	MV	ML+	MN+	MO+	MC	MN	MO	MN+	MO+	MR+
Salmonidae	*Oncorhynchus mykiss*	3	30	24	3				4					2	1
	Salmo trutta		11	7	4	1			5					2	
Cyprinidae	*Barbonymus gonionotus*		2												
	Carassius auratus	1		1	1										
	Ctenopharyngodon idella	6	9	23	7			2	7						
	Cyprinus carpio	3	6	44	22		2	1	5				1		
Xenocyprididae	*Hypophthalmichthys molitrix*	2	15	17	2				2			4			
	Hypophthalmichthys nobilis	2	4	8				1	3			4			
Clariidae	*Clarias gariepinus*	2	17	2	1										
Loricariidae	*Pterygoplichthys disjunctivus*		3								2				
Serrasalmidae	*Piaractus brachypomus*		6												
Poeciliidae	*Gambusia affinis*	3	8	2									2		
	Poecilia reticulata	1	4		1										
Cichlidae	*Oreochromis mossambicus*	2	21	1	1					1					
	Oreochromis niloticus	3	28	14	5	1			2	2	1		1	1	

Figure 1. Detrimental and beneficial environmental (EICAT and EICAT+) and socio-economic impacts (SEICAT and SEICAT+) of the 15 NNF species with reported impacts. Impact magnitude ranges from Minimal Concern (MC), Minor (MN), Moderate (MO) and Major (MR) to Massive (MV). The colour intensity increases with impact severity. Numbers indicate the number of impact records for each species and impact magnitude.

negative environmental impacts (n = 75), including 66 strong detrimental environmental impacts (Fig. 1). Notably, detrimental environmental impacts were reported for only eight of the 15 species in India, although five of the seven species that did not show impacts in India were associated with strong impacts in the RoW (Suppl. material 1: fig. S2). Seven species had caused beneficial environmental impacts (EICAT+) (Fig. 1). Additionally, five species had caused detrimental socio-economic impacts and five species beneficial socio-economic impacts (Fig. 1). While *H. molitrix* and *H. nobilis* had multiple strong detrimental socio-economic impacts (MO), the introduction of rainbow and brown trout in the USA and South Africa had strong beneficial socio-economic impacts (Fig. 1). Of all species, only *Oreochromis niloticus* had reported detrimental and beneficial environmental and socio-economic impacts (Fig. 1).

Detrimental impacts on vertebrates were frequent (57% i.e. 218 of 384 records), with predation (n = 142) being the most frequent mechanism (Suppl. material 1: figs S4, S5). In contrast, most beneficial impacts (62% i.e. 21 of 34 records) were reported for invertebrates, with 'Indirect impacts through interactions with other taxa' being the most frequent mechanism (Suppl. material 1: table S4). Socio-economic impacts were reported for eight human community types (commercial fishers, fish consumers, fish farmers, hunters, river swimmers, recreational fishers, river boaters and village residents), while three community types (village residents, commercial and recreational fishers) experienced both detrimental and beneficial impacts (Suppl. material 1: table S5). Notably, no community undertook any 'burdensome activities' to mitigate NNF impacts. Three constituents of human well-being (i.e. safety, material and immaterial assets and health) were impacted. While most of the negative impact records involved 'safety' (57% i.e. 8 of 14 records), beneficial impact records were mostly associated with 'material and immaterial assets' (80% i.e. 8 of 10 records) (Suppl. material 1: table S5). Impacts on 'doings' (i.e. for performing an activity) were reported more frequently than impacts on 'beings', with negative impacts reported in 78% of records (11 of 14)

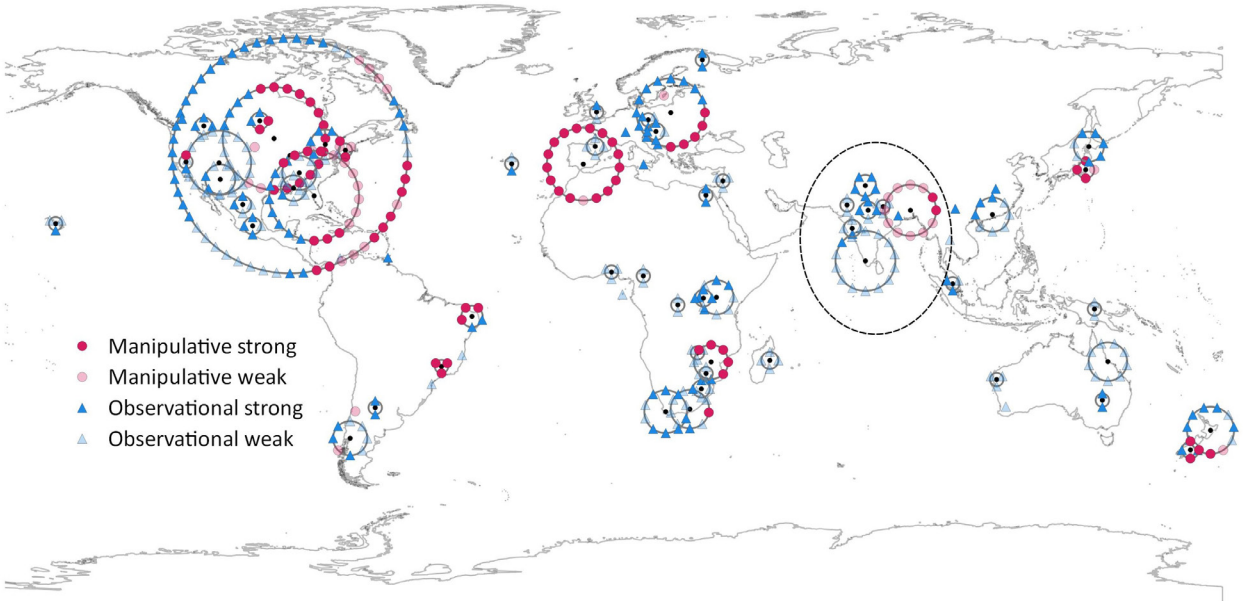

Figure 2. Spatial distribution of weak and strong environmental impacts of NNF and the study types (observational/manipulative) that reported these environmental impacts (n = 418). The map shows that strong impacts reported from manipulative studies are mostly concentrated in North America and Western Europe. Observational studies are dominant in India (highlighted in dotted circle). Point locations with clustered or overlapping impacts are displaced into non-overlapping circles to improve visual clarity.

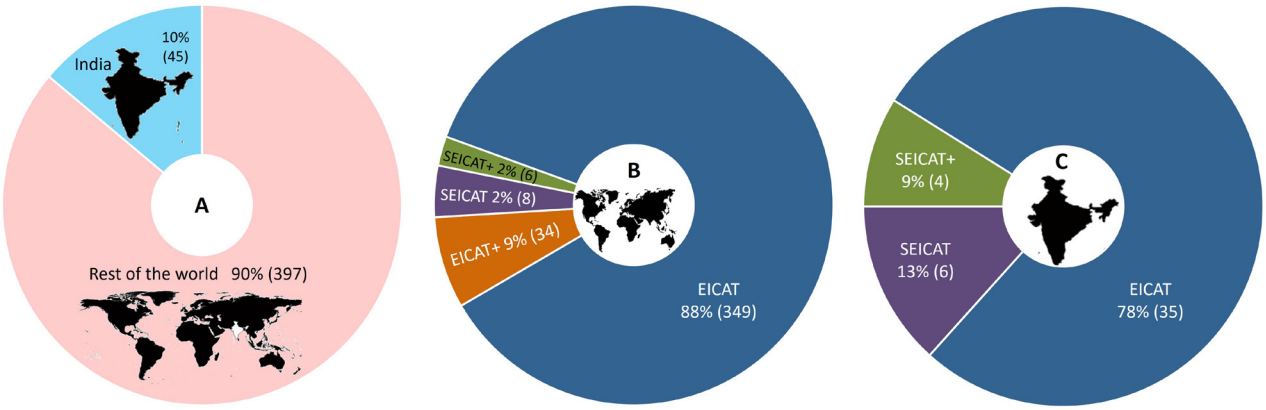

Figure 3. A. Distribution of documented detrimental and beneficial environmental and socio-economic impacts of NNF across India and the RoW (n = 442); **B.** Distribution of documented detrimental environmental impacts (EICAT) compared to documented beneficial environmental impacts (EICAT+), detrimental socio-economic impacts (SEICAT) and beneficial socio-economic impacts (SEICAT+) in the RoW (n = 397); **C.** Distribution of documented detrimental environmental and socio-economic impact records in India (n = 45). Note that no beneficial environmental impacts (EICAT+) were reported in India in the available literature.

and positive impacts in 70% of records (7 of 10) (Suppl. material 1: table S5). Spatially, a high number of environmental impacts, both detrimental (40% i.e. 156 of 384 records) and beneficial (44% i.e. 15 of 34 records), as well as detrimental socio-economic impacts (57% i.e. 8 of 14 records) were reported from the Nearctic realm, whereas highest number of beneficial socio-economic impacts (50% i.e. 5 of 10 records) were reported from the Ethiopian realm (Suppl. material 1: fig. S6).

We obtained eight models with different combinations of variables, four of which had a ΔAICc < 6 in relation to the best model (Table 2). The variables 'impacted groups' and 'impact location' showed sufficient explanatory power (relative importance > 0.5; Suppl. material 1: table S6) and were included in the model with lowest AICc (Table 2),

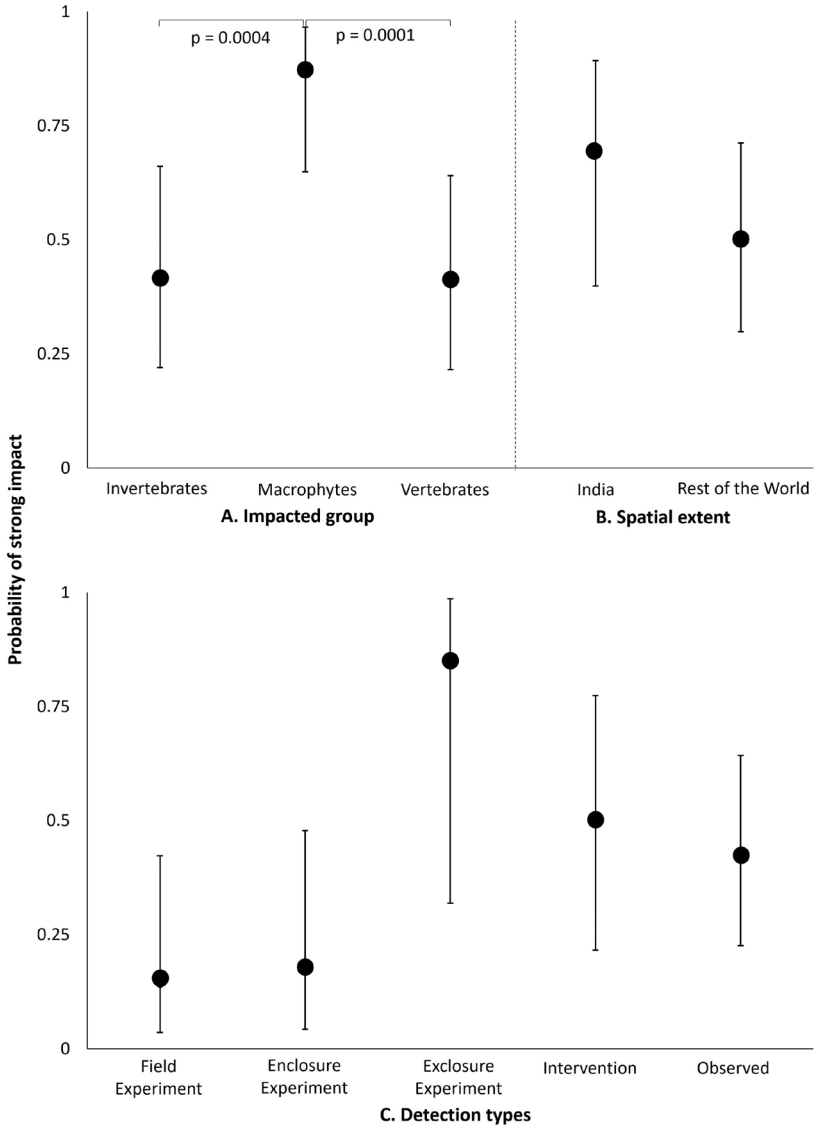

Figure 4. Post-hoc pairwise comparisons of probability of (**A**) strong detrimental environmental impacts of NNF with impacted groups: invertebrates (n = 98), macrophytes (n = 68) and vertebrates (n = 218) from the most-supported model, (**B**) strong detrimental environmental impacts of NNF in spatial extent: India (n = 34), the RoW (n = 349) from the most-supported model, (**C**) strong environmental impacts of NNF with detection types: Field experiment (n = 27), Enclosure experiment (n = 18), Exclosure experiment (n = 8), Intervention (n = 49) and Observed (n = 304). Points are estimated marginal means with 95% Confidence Intervals. Horizontal brackets are pairwise comparisons and values are p-values indicating significant differences.

which was considered as the most supported model. NNF were significantly more likely to cause strong detrimental impacts on macrophytes compared to vertebrates and invertebrates (Fig. 4A, Suppl. material 1: table S7). In contrast, the probability of strong detrimental environmental impacts did not differ significantly between intra- and inter-realm transfers (transfer type) or between India and the RoW (impact location) (Fig. 4B, Suppl. material 1: table S7), and this pattern remained when analysing the reduced dataset only (i.e., dataset with the NNF present in both India and the Row). Further, the probability of reporting strong environmental impacts did not differ significantly among detection types (Fig. 4C, Suppl. material 1: table S7). Fisher's exact test showed a significant association between study type (observational/manipulative) and impact location (India/

Table 2. Best-fitting generalized linear mixed-effect models (ΔAICc < 6) predicting strong impact of NNF with species name and impacted realm as random effects. df: degrees of freedom, AICc: corrected Akaike Information Criterion, weight: Akaike weight. Predictors- IG: impacted group, IL: impact location, TT: transfer type.

Fixed effects	df	AICc	ΔAICc	Weight	Evidence ratio
IG, IL (Best fit)	6	444.8	0	0.386	1
IG	5	445.1	0.27	0.336	1.15
IG, IL, TT	7	446.8	1.96	0.145	2.66
IG, TT	6	447	2.14	0.132	2.92

RoW) ($p < 0.001$), indicating that the odds of a study being observational in India is 6.8 times higher compared to the RoW (Suppl. material 1: table S8).

Discussion

We assessed both detrimental and beneficial environmental and socio-economic impacts of 20 most widely distributed NNF in India, making it the first study to apply all four ICAT frameworks (EICAT, EICAT+, SEICAT and SEICAT+). We found no relevant impact data for five NNF, while 15 NNF had documented impacts that varied across impact types, species and regions. As expected, native macrophytes was the group most strongly negatively impacted by NNF, whereas, contrary to our hypotheses, the model suggested no significant difference between inter- and intra-realm transfer (transfer type), and between India and the RoW (impact location). Also contrary to our expectation, there was no significant difference in detecting strong environmental impacts between detection types (different manipulative methods and observations).

Patterns in the impact data

Most impact records (87%) in our dataset were detrimental environmental impacts, thus aligning with global cross-taxonomic trends, where 85% of documented environmental impacts of invasive non-native species were detrimental to nature (Bacher et al. 2023). This pattern is also consistent with a recent study on non-native large mammalian herbivores, which found that 80% of all reported impacts on native biodiversity were detrimental (Bescond-Michel et al. 2025). A global study of impacts of non-native megafish species even found 97% of documented environmental impacts to be detrimental (Chen et al. 2024). Additionally, the Global Impacts Dataset of Invasive Alien Species (GIDIAS) reported more environmental impact records (13221 impact records; 80%) than human well-being impact records (3302 impact records; 20%) across all non-native taxa combined, where impacts on good quality of life were derived using SEICAT framework (Bacher et al. 2025). This is consistent with our dataset which had fewer socio-economic impact records (24 impact records; 5%) than environmental impact records (418 impact records; 95%). Further, our dataset reflects the global pattern of invasive non-native species impact data being more abundant in the Global North (Bacher et al. 2023, 2025). Similar trends were observed by Chen et al. (2024) on impacts of non-native megafish species who reported that Africa, South America and large parts of Asia had fewer environmental impact records than the Global North, with fewer positive environmental impacts than negative ones.

Chen et al. (2024) independently assessed the environmental impacts of non-native megafish species using the EICAT and EICAT+ frameworks. Seven of these species overlapped with those included in the present study. A comparison of the maximum impact scores assigned to these species across both EICAT and EICAT+ revealed that six of the fourteen assessments were identical between the two studies (Suppl. material 1: table S1). In addition, 19 of the 20 NNF assessed in the present study were also included in the GIDIAS dataset (Bacher et al. 2025). The GIDIAS database had captured a larger number of reports than our initial dataset. By cross-referencing with GIDIAS, we added an additional 45 reports resulting in inclusion of 105 EICAT, 3 EICAT+ and 4 SEICAT+ impact records into our dataset and analysis. The differences among the studies in the identified literature sources are likely due to (a) different points in time when the literature searches were carried out, (b) different search strategies and (c) involvement of regional experts across the world in the GIDIAS assessments who may have identified additional local or regional reports. Furthermore, a detailed investigation of the underlying reasons for differences in impact scores could be addressed in future research, then jointly with other studies who applied the ICAT framework for overlapping species.

In our assessments, massive impacts (MV) were caused by brown trout and Nile tilapia. Nile tilapia has been linked to the extinction of the short-barbelled barb, *Labeobarbus microbarbis*, a fish species endemic to Lake Luhondo in Rwanda. Alternative explanations such as over-exploitation or disease have been ruled out, leaving the introduction of Nile tilapia as the most plausible driver of extinction (De Vos et al. 1990). Following Nile tilapia's introduction, the lake ecosystem shifted from a clear-water system with abundant submerged vegetation to a more turbid state lacking submerged macrophytes, altering habitat structure and resource availability for short-barbelled barb (De Vos et al. 1990). Similarly, brown trout caused the global extinction of the New Zealand grayling—a fish endemic to New Zealand. Predation and competition from brown trout were identified as contributing factors (McDowall 1990) alongside other stressors (over-exploitation, habitat change, etc.) (Townsend 1996). However, Lee and Perry (2019) found that trout introduction was cited as frequently as all other drivers combined for the extinction of the grayling, underlining the importance of brown trout for this extinction. Brown trout was also found to benefit the native zooplankton and chironomids by increasing their abundance through a trophic cascade effect (MO+) (Nyström and McIntosh 2003; Milardi et al. 2016). Further, rainbow trout was the only species with a positive major socio-economic impact, but it also had strong detrimental environmental impacts. Introduction of rainbow trout downstream of the Glen Canyon Dam in the Colorado River (USA) established rainbow trout fishery (appearance of a new activity; MR+), with electrofishing surveys in 2018 showing that rainbow trout comprised up to 98% of the fish community by numbers (Bair et al. 2016; Boyer and Rogowski 2019). An estimated 7347 anglers (recreational fishers) visited the area for fishing in 2018 (Boyer and Rogowski 2019), and the net value of rainbow trout fishery in 2014 was estimated at 2.7 million US$ there (Bair et al. 2016). This highlights the positive impact of rainbow trout introduction for the anglers and on the region's economy. In contrast, rainbow trout negatively affected populations of native fish and invertebrates; for example, predation by rainbow trout resulted in the local extirpation (MR) of Breede River redfin (*Pseudobarbus burchelli*), Cape kurper (*Sandelia capensis*) and Cape galaxias (*Galaxias zebratus*) in the Breede River catchment, South Africa (Shelton et al. 2015).

Common carp is one of the globally most widely introduced NNF (140 river basins; Chen et al. 2024) for which we found the highest number of documented impact records (84). Most of these records were detrimental to native species (75), including 66 strong detrimental impacts. Common carp caused local extirpation (MR) of macrophytes in most cases (18 of 22 MR records), mainly reported in the USA (e.g., Lougheed et al. 1998; Bajer et al. 2016). Its negative impacts through population declines of native species were evident across invertebrates, vertebrates, and macrophytes, with most of these impacts having been documented in North America (24 of 44 MO records; Suppl. material 2). Nile tilapia was the only species with documented positive and negative environmental and socio-economic impacts. While being widely introduced (El-Sayed and Fitzsimmons 2023), this species is regarded as one of the most economically important fishes in freshwater aquaculture (FAO 2020). While Nile tilapia has been linked to the extinction of short barbelled barb in Africa, population declines of native invertebrates and vertebrates (MO) have also been reported in India, Brazil and China (Attayde et al. 2011; Shuai et al. 2019; Johnson et al. 2020). In contrast, an in-situ mesocosm experiment in Brazil recorded increased abundance of plankton (MO+) (Figueredo and Giani 2005). Notably, all documented negative and positive socio-economic impacts of Nile tilapia have been documented in India, but only one detrimental environmental impact of brown trout has been documented in India (Sharma et al. 2021), and no impacts were documented for common carp and rainbow trout, although both species are widespread in the country.

Commercial and recreational fishers experienced both detrimental and beneficial impacts from NNF introductions. In India, commercial fishers reported economic losses from reduced fish catch caused by Mozambique and Nile tilapia (Dwivedi et al. 2014; Regi and Biju Kumar 2018). They also reported damaged fishing nets leading to longer fishing hours due to Amazon sailfin catfish (*Pterygoplichthys disjunctivus*) (Seshagiri et al. 2021). In contrast, benefits were noted from Nile tilapia in Halali reservoir, India (Johnson et al. 2020), and common carp in Lake Naivasha, Kenya (Hickley et al. 2015), which supported employment and income. Further, silver and bighead carps reduced the number of recreational fishers in La Grange Reach, Illinois River, USA (Spacapan et al. 2016), while rainbow trout introductions in the Colorado River created a trout fishery attracting thousands of recreational fishers (Bair et al. 2016). Some people reported health concerns (MC) because eating contaminated NNF exposed them to heavy metals (Singh et al. 2014). Commercial fishers also noted a decline in income due to declining fish catches resulting from the spread of NNF (Regi and Biju Kumar 2018). Conversely, people reported improvements to their health after the introduction of mosquito fish (*Gambusia affinis*) which contributed to reduction of vector-borne diseases (Singh et al. 2022). This highlights that perception of NNF impacts may vary with NNF species, people, region and context.

Factors associated with strong detrimental environmental impacts

Our model supported the hypothesis that NNF exert stronger negative impacts on macrophytes than on animals. Gallardo et al. (2016) investigated the impacts of non-native species in aquatic ecosystems and found that omnivores and herbivores caused the greatest reductions in macrophyte abundance. In our dataset, macrophytes were impacted by three species: grass carp (*Ctenopharyngodon idella*), pirapitinga (*Piar-*

actus brachypomus) and common carp, of which the former is herbivore and the latter two are omnivores (Froese and Pauly 2025). While herbivorous fishes reduce macrophytes mainly through grazing, omnivores cause impacts on macrophytes by bioturbating sediments, uprooting plants while foraging, and resuspending sediments that limit light penetration (Cucherousset and Olden 2011; Bajer et al. 2016; Gallardo et al. 2016). Accordingly, our results showed that herbivores impacted macrophytes mainly through direct grazing, producing a mix of weak and strong impacts (6 weak and 24 strong impacts). In contrast, omnivores impacted macrophytes through physical disturbances (bioturbation, uprooting), resulting almost exclusively in strong impacts (37 strong of 38 impact records). This may reflect a detection bias: impacts on macrophytes, such as reduction in cover, biomass, or species richness, are easier to observe and quantify compared to vertebrates and invertebrates, which are mobile and thus more difficult to study (Kellner and Swihart 2014).

The probability of strong detrimental environmental impacts was similar between India and the RoW, despite the scarcity of studies on NNF impacts in India (Kumar et al. 2025). No detrimental environmental impact data was available for seven NNF from India, despite strong impacts, including local extirpations, being reported for these species in the RoW. Additionally, although our findings indicate that macrophytes are the most impacted group, none of the impact records on macrophytes were from India. Therefore, under the assumptions that NNF impacts in India are understudied but not different from those that occur in the RoW, we suggest that research of NNF in India should focus on impact assessments to rank NNF by their detrimental impacts to help prioritization for management. Unless we have more information, NNF management is advised to adopt a precautionary approach, which emphasizes that in the absence of impact data for a region the highest documented EICAT impacts from elsewhere can guide decision making (Kumschick et al. 2024).

Role of methodological approaches in impact detection

Contrary to our hypothesis, we found no significant difference among detection types in their likelihood of detecting strong environmental impacts of NNF. This contrasts with previous studies that suggested an influence of study design on the detection of environmental impacts (Závorka et al. 2018; Jakubavičiūtė et al. 2025).

We found that observational studies were predominant in India. A systematic review of freshwater NNF in India revealed that of the studies that assessed the impacts of NNF, most employed an observational approach (46 of 62 studies) (Kumar et al. 2025). Further, Thomsen et al. (2014) reviewed manipulative studies in aquatic invasive species over four decades and found that more than half of the experiments were conducted in the USA (53%) followed by Europe and Oceania. Thus, our finding that observational studies were more common in India is consistent with this broader pattern. These results are important especially for countries like India, where resources are limited and observational studies are predominant, because they might encourage more experimental study designs and addressing taxonomic groups with no documented impacts.

Way forward

Our study represents one of the most comprehensive and holistic assessments of NNF impacts to date, as it encompasses both detrimental and beneficial environmental and socio-economic impacts at the global scale. At the same time, it

specifically focused on India, a large country with critical research gaps, serving as a model for many other heavily understudied countries of the Global South. Looking ahead, while we globally recommend prioritising the conservation of macrophytes, management should ideally consider contextual environmental and socio-economic aspects. Also, we do not suggest that native animal groups other than macrophytes are free from risk, as our results indicated strong impacts in those instances as well, thus stressing the necessity of a continued, broad baseline surveillance across various contexts. Higher investments in invasion research in the Global South or use of funds from wealthier countries to build strong international collaborations are needed to reduce geographic research gaps on biological invasions. In conclusion, future research on the bidirectional impacts that non-native species have on biodiversity and human well-being promises to enrich ICAT assessments and contributes to the growing knowledge base of impacts of non-native species (Bacher et al. 2025). Such research will facilitate impact comparisons across taxa and regions, and support evidence-based decision making for the management of NNF in India and elsewhere.

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References

Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. The Journal of Wildlife Management 66: 912–918. https://doi.org/10.2307/3803155

Attayde JL, Brasil J, Menescal RA (2011) Impacts of introducing Nile tilapia on the fisheries of a tropical reservoir in North-eastern Brazil. Fisheries Management and Ecology 18: 437–443. https://doi.org/10.1111/j.1365-2400.2011.00796.x

Bacher S, Galil BS, Nuñez MA, Ansong M, Cassey P, Dehnen-Schmutz K, Fayvush G, Hiremath AJ, Ikegami M, Martinou AF, McDermott SM, Preda C, Vilà M, Weyl OLF, Fernandez RD, Ryan-Colton E, Rai RK, Richardson DM (2023) IPBES Invasive alien species assessment: chapter 4. Impacts of invasive alien species on nature, nature's contributions to people, and good quality of life. Zenodo 4. https://doi.org/10.5281/ZENODO.10677193

Bacher S, Blackburn TM, Essl F, Genovesi P, Heikkilä J, Jeschke JM, Jones G, Keller R, Kenis M, Kueffer C, Martinou AF, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roy HE, Saul W-C, Scalera R, Vilà M, Wilson JRU, Kumschick S (2018) Socio-economic impact classification of alien taxa (SEICAT). Methods in Ecology and Evolution 9: 159–168. https://doi.org/10.1111/2041-210X.12844

Bacher S, Ryan-Colton E, Coiro M, Cassey P, Galil BS, Nuñez MA, Ansong M, Dehnen-Schmutz K, Fayvush G, Fernandez RD, Hiremath AJ, Ikegami M, Martinou AF, McDermott SM, Preda C, Vilà M, Weyl OLF, Aravind NA, Angelidou I, Athanasiou K, Atkore V, Barney JN, Blackburn TM, Brockerhoff EG, Carbutt C, Carisio L, Castro-Díez P, Céspedes V, Christopoulou A, Cisneros-Heredia DF, Cooling M, De Groot M, Demetriou J, Dickey JWE, Duboscq-Carra VG, Early R, Evans TG, Flores-Males PT, Gallardo B, Gruber M, Hui C, Jeschke JM, Joelson NZ, Khan MA, Kumschick S, Lach L, Lapin K, Lioy S, Liu C, MacMullen ZJ, Mazzitelli MA, Measey J, Mrugała-Koese AA, Musseau CL, Nahrung HF, Pepori A, Pertierra LR, Pienaar EF, Pyšek P, Rivas Torres G, Rojas Martinez HA, Rojas-Sandoval J, Ryan-Schofield NL, Sánchez RM, Santini A, Santoro D, Scalera R, Schmidt L, Shivambu TC, Sohrabi S, Tricarico E, Trillo A, Van'T Hof P,

Volery L, Zengeya TA (2025) Global impacts dataset of invasive alien species (GIDIAS). Scientific Data 12: 832. https://doi.org/10.1038/s41597-025-05184-5

Bair LS, Rogowski DL, Neher C (2016) Economic value of angling on the Colorado River at Lees Ferry: using secondary data to estimate the influence of seasonality. North American Journal of Fisheries Management 36: 1229–1239. https://doi.org/10.1080/02755947.2016.1204388

Bajer PG, Beck MW, Cross TK, Koch JD, Bartodziej WM, Sorensen PW (2016) Biological invasion by a benthivorous fish reduced the cover and species richness of aquatic plants in most lakes of a large North American ecoregion. Global Change Biology 22: 3937–3947. https://doi.org/10.1111/gcb.13377

Barton K (2019) MuMIn: multi-model inference. R package version 1.43. 17. https://doi.org/10.32614/cran.package.mumin

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01

Bellard C, Leroy B, Thuiller W, Rysman J-F, Courchamp F (2016) Major drivers of invasion risks throughout the world. Ecosphere 7: e01241. https://doi.org/10.1002/ecs2.1241

Bernery C, Bellard C, Courchamp F, Brosse S, Gozlan RE, Jarić I, Teletchea F, Leroy B (2022) Freshwater fish invasions: a comprehensive review. Annual Review of Ecology, Evolution, and Systematics 53: 427–456. https://doi.org/10.1146/annurev-ecolsys-032522-015551

Bescond-Michel Z, Bacher S, Vimercati G (2025) Harms of introduced large herbivores outweigh benefits to native biodiversity. Nature Communications 16: 8260. https://doi.org/10.1038/s41467-025-63807-2

Biggs BJ, Francoeur SN, Huryn AD, Young R, Arbuckle CJ, Townsend CR (2000) Trophic cascades in streams: effects of nutrient enrichment on autotrophic and consumer benthic communities under two different fish predation regimes. Canadian Journal of Fisheries and Aquatic Sciences 57: 1380–1394. https://doi.org/10.1139/f00-077

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A Unified classification of alien species based on the magnitude of their environmental impacts. PLOS Biology 12: e1001850. https://doi.org/10.1371/journal.pbio.1001850

Boyer JK, Rogowski DL (2019) Status of the lees ferry rainbow trout fishery 2018 annual report. Colorado River Research Office Research Branch Arizona Game and Fish Department Flagstaff AZ.

Britton JR (2023) Contemporary perspectives on the ecological impacts of invasive freshwater fishes. Journal of Fish Biology 103: 752–764. https://doi.org/10.1111/jfb.15240

Chen X, Evans TG, Jeschke JM, Jähnig SC, He F (2024) Global introductions and environmental impacts of freshwater megafish. Global Change Biology 30: e17289. https://doi.org/10.1111/gcb.17289

Chen X, Evans TG, Jeschke JM, Griffith P, Jähnig SC, He F (2026) Global assessment of alien freshwater megafauna reveals complex socio-economic impacts. One Earth 9(4): 101623. https://doi.org/10.1016/j.oneear.2026.101623

Christie AP, Amano T, Martin PA, Shackelford GE, Simmons BI, Sutherland WJ (2019) Simple study designs in ecology produce inaccurate estimates of biodiversity responses. Journal of Applied Ecology 56: 2742–2754. https://doi.org/10.1111/1365-2664.13499

Cucherousset J, Olden JD (2011) Ecological impacts of non-native freshwater fishes. Fisheries 36: 215–230. https://doi.org/10.1080/03632415.2011.574578

De Vos L, Snoeks J, Van Den Audenaerde DT (1990) The effects of *Tilapia* introductions in lake Luhondo, Rwanda. Environmental Biology of Fishes 27: 303–308. https://doi.org/10.1007/BF00002748

Diamond J, Case TJ (1986) Overview: introductions, extinctions, exterminations, and invasions. In: Diamond J, Case TJ (Eds) Community Ecology. Harper and Row, New York.

Drake DL, Anderson TL, Smith LM, Lohraff KM, Semlitsch RD (2014) Predation of eggs and recently hatched larvae of endemic ringed salamanders (*Ambystoma annulatum*) by native and introduced aquatic predators. Herpetologica 70: 378–387. https://doi.org/10.1655/herpetologica-d-14-00017

Dwivedi AC, Jha DN, Mayank P (2014) Food security, livelihood and non-native fish species: status, trends and future perspectives. Journal of the Kalash Science 2: 41–46.

El-Sayed AM, Fitzsimmons K (2023) From Africa to the world—The journey of Nile tilapia. Reviews in Aquaculture 15: 6–21. https://doi.org/10.1111/raq.12738

Enders M, Havemann F, Ruland F, Bernard-Verdier M, Catford JA, Gómez-Aparicio L, Haider S, Heger T, Kueffer C, Kühn I, Meyerson LA, Musseau C, Novoa A, Ricciardi A, Sagouis A, Schittko C, Strayer DL, Vilà M, Essl F, Hulme PE, van Kleunen M, Kumschick S, Lockwood JL, Mabey AL, McGeoch MA, Palma E, Pyšek P, Saul W-C, Yannelli FA, Jeschke JM (2020) A conceptual map of invasion biology: Integrating hypotheses into a consensus network. Global Ecology and Biogeography 29: 978–991. https://doi.org/10.1111/geb.13082

Evans T, Kumschick S, Blackburn TM (2016) Application of the environmental impact classification for alien taxa (EICAT) to a global assessment of alien bird impacts. Diversity and Distributions 22: 919–931. https://doi.org/10.1111/ddi.12464

FAO (2020) World fisheries and aquaculture. Food and Agriculture Organization 2020: 1–244.

Figueredo CC, Giani A (2005) Ecological interactions between Nile tilapia (*Oreochromis niloticus*, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). Freshwater Biology 50: 1391–1403. https://doi.org/10.1111/j.1365-2427.2005.01407.x

Flecker AS, Townsend CR (1994) Community-wide consequences of trout introduction in New Zealand streams. Ecological Applications 4: 798–807. https://doi.org/10.2307/1942009

Forgione L, Bacher S, Vimercati G (2022) Are species more harmful in their native, neonative or alien range? Insights from a global analysis of bark beetles. Diversity and Distributions 28: 1832–1849. https://doi.org/10.1111/ddi.13585

Froese R, Pauly D (2025) FishBase. https://www.fishbase.se/ [June 13, 2025]

Galanidi M, Zenetos A, Bacher S (2018) Assessing the socio-economic impacts of priority marine invasive fishes in the Mediterranean with the newly proposed SEICAT methodology. Mediterranean Marine Science 19: 107–123. https://doi.org/10.12681/mms.15940

Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology 22: 151–163. https://doi.org/10.1111/gcb.13004

González-Moreno P, Lazzaro L, Vilà M, Preda C, Adriaens T, Bacher S, Brundu G, Copp GH, Essl F, García-Berthou E, Katsanevakis S, Moen TL, Lucy FE, Nentwig W, Srebaliene G, Roy HE, Talgø V, Vanderhoeven S, Andjelkovic A, Arbaciauskas K, Auger-Rozenberg MA, Bae MJ, Bariche M, Boets P, Boieiro M, Borges PAV, Canning-Clode J, Cardigos F, Chartosia N, Cottier-Cook EJ, Crocetta F, D'hondt B, Foggi B, Follak S, Gallardo B, Gammelmo Ø, Giakoumi S, Giuliani C, Guillaume F, Jelaska LŠ, Jeschke JM, Jover M, Juárez-Escario A, Kalogirou S, Kocic A, Kytinou E, Laverty C, Lozano V, Maceda-Veiga A, Marchante E (2019) Consistency of impact assessment protocols for non-native species. NeoBiota 44: 1–25. https://doi.org/10.3897/neobiota.44.31650

Hartig F (2024) DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) Regression Models. R package version 0.4.7. https://doi.org/10.32614/cran.package.dharma

Haubrock PJ, Copp GH, Johović I, Balzani P, Inghilesi AF, Nocita A, Tricarico E (2021) North American channel catfish, *Ictalurus punctatus*: a neglected but potentially invasive freshwater fish species? Biological Invasions 23: 1563–1576. https://doi.org/10.1007/s10530-021-02459-x

Hickley P, Britton JR, Macharia S, Muchiri SM, Boar RR (2015) The introduced species fishery of Lake Naivasha, Kenya: ecological impact vs socio-economic benefits. Fisheries Management and Ecology 22: 326–336. https://doi.org/10.1111/fme.12130

IUCN (2020) IUCN EICAT categories and criteria. The environmental impact classification for alien taxa. https://iucn.org/sites/default/files/2023-02/eicat-guidelines-final-v1.1.pdf

Jakubavičiūtė E, Rahman T, Candolin U (2025) Assessing the ecological impact of non-native species: single-species manipulation fails to reveal impact of invading shrimp. Biological Invasions 27: 112. https://doi.org/10.1007/s10530-025-03575-8

Johnson C, Sarkar UK, Koushlesh SK, Das AK, Das BK, Naskar BK (2020) Population structure of Nile tilapia and its impact on fisheries of a tropical impacted reservoir, Central India. Environmental Science and Pollution Research 27: 29091–29099. https://doi.org/10.1007/s11356-020-09234-w

Kadye WT, Chakona A, Marufu LT, Samukange T (2013) The impact of non-native rainbow trout within Afro-montane streams in eastern Zimbabwe. Hydrobiologia 720: 75–88. https://doi.org/10.1007/s10750-013-1624-4

Kellner KF, Swihart RK (2014) Accounting for imperfect detection in ecology: A quantitative review. PLOS ONE 9: e111436. https://doi.org/10.1371/journal.pone.0111436

Kumar L, Ruland F, Jeschke JM (2025) Non-native freshwater fishes in India: existing evidence and knowledge gaps. NeoBiota 102: 419–440. https://doi.org/10.3897/neobiota.102.146421

Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugała A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. BioScience 65: 55–63. https://doi.org/10.1093/biosci/biu193

Kumschick S, Bertolino S, Blackburn TM, Brundu G, Costello KE, De Groot M, Evans T, Gallardo B, Genovesi P, Govender T, Jeschke JM, Lapin K, Measey J, Novoa A, Nunes AL, Probert AF, Pyšek P, Preda C, Rabitsch W, Roy HE, Smith KG, Tricarico E, Vilà M, Vimercati G, Bacher S (2024) Using the IUCN environmental impact classification for alien taxa to inform decision-making. Conservation Biology 38: e14214. https://doi.org/10.1111/cobi.14214

Lee F, Perry GLW (2019) Assessing the role of off-take and source–sink dynamics in the extinction of the amphidromous New Zealand grayling (*Prototroctes oxyrhynchus*). Freshwater Biology 64: 1747–1754. https://doi.org/10.1111/fwb.13366

Lenth R (2025) emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.11.1. https://CRAN.R-project.org/package=emmeans

Leroy B, Dias MS, Giraud E, Hugueny B, Jézéquel C, Leprieur F, Oberdorff T, Tedesco PA (2019) Global biogeographical regions of freshwater fish species. Journal of Biogeography 46: 2407–2419. https://doi.org/10.1111/jbi.13674

Lougheed VL, Crosbie B, Chow-Fraser P (1998) Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. Canadian Journal of Fisheries and Aquatic Sciences 55: 1189–1197. https://doi.org/10.1139/f97-315

Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3: 182–196. https://doi.org/10.1002/ece3.431

Maceda-Veiga A, López R, Green AJ (2017) Dramatic impact of alien carp *Cyprinus carpio* on globally threatened diving ducks and other waterbirds in Mediterranean shallow lakes. Biological Conservation 212: 74–85. https://doi.org/10.1016/j.biocon.2017.06.002

McDowall RM (1990) New Zealand freshwater fishes: A natural history and guide. Auckland, New Zealand: Heinemann Reed. https://doi.org/10.1007/978-90-481-9271-7

Milardi M, Siitonen S, Lappalainen J, Liljendahl A, Weckström J (2016) The impact of trout introductions on macro- and micro-invertebrate communities of fishless boreal lakes. Journal of Paleolimnology 55: 273–287. https://doi.org/10.1007/s10933-016-9879-1

Nyström P, McIntosh AR (2003) Are impacts of an exotic predator on a stream food web influenced by disturbance history? Oecologia 136: 279–288. https://doi.org/10.1007/s00442-003-1250-3

Olden JD, Kennard MJ, Pusey BJ (2008) Species invasions and the changing biogeography of Australian freshwater fishes. Global Ecology and Biogeography 17: 25–37. https://doi.org/10.1111/j.1466-8238.2007.00340.x

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Holle BV, Moyle PB, Byers JE, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19. https://doi.org/10.1023/a:1010034312781

Probert AF, Volery L, Kumschick S, Vimercati G, Bacher S (2020) Understanding uncertainty in the impact classification for alien taxa (ICAT) assessments. NeoBiota 62: 387–405. https://doi.org/10.3897/neobiota.62.52010

Probert AF, Vimercati G, Kumschick S, Volery L, Bacher S (2023) Clarification and guidance on the use of the socio-economic impact classification for alien taxa (SEICAT) framework. NeoBiota 89: 45–70. https://doi.org/10.3897/neobiota.89.109911

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Raj S, Devi S, Salam S, Kumar AB (2021) Food spectrum of two co-occurring invasive fish, *Cyprinus carpio* Linnaeus, 1758 and *Clarias gariepinus* (Burchell, 1822) in Mattupetty Reservoir, Kerala, India. Indian J. Fish 68: 33–42. https://doi.org/10.21077/ijf.2021.68.2.101875-05

Regi SR, Biju Kumar A (2018) Trophic impact of invasive mosambique tilapia *Oreochromis mossambicus* on indigenous fish groups in Veli-Akkulam Lake, Kerala, India: an ecopath modeling approach. Proceedings International Biodiversity Congress (IBC) 2018 IV: 476–483.

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7: 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x

Richards SA (2008) Dealing with overdispersed count data in applied ecology. Journal of Applied Ecology 45: 218–227. https://doi.org/10.1111/j.1365-2664.2007.01377.x

Roshni K, Renjithkumar CR, Sreekanth GB, Raghavan R, Ranjeet K, Harikrishnan M, Kurup BM (2021) Trophic interactions between native and exotic cichlids in a shallow tropical estuary (Lake Vembanad, India). Marine and Freshwater Research 73: 411–416. https://doi.org/10.1071/MF21044

Saul W, Jeschke JM (2015) Eco-evolutionary experience in novel species interactions. Eubanks M (Ed.). Ecology Letters 18: 236–245. https://doi.org/10.1111/ele.12408

Seshagiri B, Swain SK, Pillai BR, Satyavati C, Sravanti Y, Rangacharyulu PV, Rathod R, Ratnaprakash V (2021) Suckermouth armoured catfish (*Pterygoplichthys* spp.) menace in freshwater aquaculture and natural aquatic systems in Andhra Pradesh, India. International Journal of Fisheries and Aquatic Studies 9: 375–384. https://doi.org/10.22271/fish.2021.v9.i1e.2423

Sharma A, Dubey VK, Johnson JA, Rawal YK, Sivakumar K (2021) Dendritic prioritization through spatial stream network modeling informs targeted management of Himalayan riverscapes under brown trout invasion. Journal of Applied Ecology 58: 2415–2426. https://doi.org/10.1111/1365-2664.13997

Shelton JM, Samways MJ, Day JA (2015) Predatory impact of non-native rainbow trout on endemic fish populations in headwater streams in the Cape Floristic Region of South Africa. Biological Invasions 17: 365–379. https://doi.org/10.1007/s10530-014-0735-9

Shuai F, Li X, Liu Q, Zhu S, Wu Z, Zhang Y (2019) Nile tilapia (*Oreochromis niloticus*) invasions disrupt the functional patterns of fish community in a large subtropical river in China. Fisheries Management and Ecology 26: 578–589. https://doi.org/10.1111/fme.12368

Singh AK, Srivastava SC, Ansari A, Kumar D, Singh R (2012) Environmental Monitoring and health risk assessment of African catfish *Clarias gariepinus* (Burchell, 1822) cultured in rural ponds, India. Bulletin of Environmental Contamination and Toxicology 89: 1142–1147. https://doi.org/10.1007/s00128-012-0860-z

Singh AK, Srivastava SC, Verma P, Ansari A, Verma A (2014) Hazard assessment of metals in invasive fish species of the Yamuna River, India in relation to bioaccumulation factor and exposure concentration for human health implications. Environmental Monitoring and Assessment 186: 3823–3836. https://doi.org/10.1007/s10661-014-3660-6

Singh H, Gupta SK, Vikram K, Saxena R, Srivastava A, Nagpal BN (2022) Sustainable control of malaria employing Gambusia fishes as biological control in Jalore and Barmer districts of Western Rajasthan. Journal of Vector Borne Diseases 59: 91. https://doi.org/10.4103/0972-9062.346869

Spacapan MM, Besek JF, Sass GG (2016) Perceived influence and response of river users to invasive bighead and silver carp in the Illinois River. Technical Report INHS 2016 (20). https://hdl.handle.net/2142/90061 [July 14, 2025]

Tarkan AS, Emiroğlu Ö, Aksu S, Başkurt S, Aksu İ, Vilizzi L, Yoğurtçuoğlu B (2022) Coupling molecular and risk analysis to investigate the origin, distribution and potential impact of non-native species: an application to ruffe *Gymnocephalus cernua* in Turkey. The European Zoological Journal 89: 109–121. https://doi.org/10.1080/24750263.2021.2022222

Thomsen M, Wernberg T, Olden J, Byers JE, Bruno J, Silliman B, Schiel D (2014) Forty years of experiments on aquatic invasive species: are study biases limiting our understanding of impacts? NeoBiota 22: 1–22. https://doi.org/10.3897/neobiota.22.6224

Townsend CR (1996) Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. Biological Conservation 78: 13–22. https://doi.org/10.1016/0006-3207(96)00014-6

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, Partners D (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8: 135–144. https://doi.org/10.1890/080083

Vimercati G, Kumschick S, Probert AF, Volery L, Bacher S (2020) The importance of assessing positive and beneficial impacts of alien species. NeoBiota 62: 525–545. https://doi.org/10.3897/neobiota.62.52793

Vimercati G, Probert AF, Volery L, Bernardo-Madrid R, Bertolino S, Céspedes V, Essl F, Evans T, Gallardo B, Gallien L, González-Moreno P, Grange MC, Hui C, Jeschke JM, Katsanevakis S, Kühn I, Kumschick S, Pergl J, Pyšek P, Rieseberg L, Robinson TB, Saul W-C, Sorte CJB, Vilà M, Wilson JRU, Bacher S (2022) The EICAT+ framework enables classification of positive impacts of alien taxa on native biodiversity. PLOS Biology 20: e3001729. https://doi.org/10.1371/journal.pbio.3001729

Vimercati G, Probert A, Kumschick S, Bacher S (2025) SEICAT+: a comprehensive assessment framework for positive socio-economic impacts of alien species. EcoEvoRxiv. https://doi.org/10.32942/X28M09

Volery L, Blackburn TM, Bertolino S, Evans T, Genovesi P, Kumschick S, Roy HE, Smith KG, Bacher S (2020) Improving the environmental impact classification for alien taxa (EICAT): a summary of revisions to the framework and guidelines. NeoBiota 62: 547–567. https://doi.org/10.3897/neobiota.62.52723

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://doi.org/10.1007/978-0-387-98141-3

Závorka L, Buoro M, Cucherousset J (2018) The negative ecological impacts of a globally introduced species decrease with time since introduction. Global Change Biology 24: 4428–4437. https://doi.org/10.1111/gcb.14323

Supplementary material 1

Supplementary tables S1–S8, figures S1–S6

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Data type: docx

Explanation note: Manipulative methods.

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Supplementary material 2

Supplementary tables S9, S10

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Data type: xlsx

Explanation note: ICAT assesments.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
The AI tool embedded in Microsoft Word was used to detect spelling mistakes and improve the language. GitHub Copilot was used to assist with R code generation and code completion.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.