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Worldwide Invasions of Centrarchidae: The Dark Side of the Sunfish Family

Neil Angelo Abreo^{1,2}  | Jonathan Tibo³  | António Barbosa Nogueira⁴  | Athanasios Nikolaou⁵  | Cüneyt Kaya⁶  | Ali Serhan Tarkan^{7,8}  | Irmak Kurtul^{9,10}  | Stelios Katsanevakis⁵  | Ronaldo Sousa⁴  | Teun Everts^{3,11}  | Emili García-Berthou¹²  | John S. Hargrove^{13,14}  | Ana Clara Sampaio Franco¹²  | Jelger Erik Herder¹⁵  | Julian D. Olden¹⁶  | Darragh J. Woodford^{14,17}  | Antonin Kouba¹  | J. Rob Britton¹⁰  | Ismael Soto¹  | Phillip J. Haubrock^{1,10} 

¹Faculty of Fisheries and Protection of Waters, South Bohemian Research Centre of Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in České Budějovice, Vodňany, Czech Republic | ²College of Health Sciences, Mapua Malayan Colleges, Mindanao, Philippines | ³Biology Department, KU Leuven, Heverlee, Belgium | ⁴CBMA—Centre for Molecular and Environmental Biology/ARNET-Aquatic Research Network & IB-S, Institute of Science and Innovation for Bio-Sustainability, Department of Biology, University of Minho, Braga, Portugal | ⁵Department of Marine Sciences, University of the Aegean, Mytilene, Greece | ⁶Faculty of Fisheries, Recep Tayyip Erdogan University, Rize, Türkiye | ⁷Faculty of Biology and Environmental Protection, Department of Ecology and Vertebrate Zoology, University of Lodz, Lodz, Poland | ⁸Department of Basic Sciences, Faculty of Fisheries, Muğla Sıtkı Koçman University, Muğla, Türkiye | ⁹Marine and Inland Waters Sciences and Technology Department, Faculty of Fisheries, Ege University, Izmir, Turkey | ¹⁰Faculty of Health, Environment and Medical Sciences, Bournemouth University, Dorset, UK | ¹¹Genetic Diversity, Research Institute for Nature and Forest, Geraardsbergen, Belgium | ¹²GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Catalonia, Spain | ¹³Pacific States Marine Fisheries Commission, Eagle, Idaho, USA | ¹⁴NRF-South African Institute for Aquatic Biodiversity, Makhanda, South Africa | ¹⁵Reptile, Amphibian and Fish Conservation Netherlands, Nijmegen, the Netherlands | ¹⁶School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA | ¹⁷Centre for Invasion Biology (C-I-B), School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

Correspondence: Neil Angelo Abreo (nabreo@jcu.cz)

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ABSTRACT

Freshwater fish invasions are major drivers of global ecological change, disrupting native biodiversity and ecosystem functions. However, many invasive fish hold significant socioeconomic value, resulting in conflict over their management. Centrarchidae, which are globally distributed and are important for sportfishing and aquaculture, are now potentially becoming a global threat. Yet, no comprehensive appraisal exists across taxa and regions integrating taxonomy, pathways, impacts and risk analysis for Centrarchidae. To address these gaps, we compiled published literature and leveraged publicly available databases to critically evaluate the current global status of non-native Centrarchidae, finding 30 species established outside their native ranges with 17 being outside of North America. Largemouth bass (*Micropterus nigricans*) and pumpkinseed (*Lepomis gibbosus*) are the most widely introduced centrarchids. Reported impacts of Centrarchidae introduction are mostly ecological, with predation, competition, hybridisation, and disease transmission as major mechanisms. Conversely, socio-economic and cultural effects are underreported. Currently, only ten species have undergone rapid risk screening, with 90% flagged as high risk. However, risk analyses remain sparse, confounded by taxonomic uncertainties (including hybridisation) and context dependence of impacts. With the changing climate and other anthropogenic disturbances in freshwaters, habitat suitability is expanding for centrarchids. Although concerning, Centrarchidae form a highly human-mediated invasion complex with predictable pathways and

Neil Angelo Abreo, Jonathan Tibo, António Barbosa Nogueira and Athanasios Nikolaou are joint first authors.
Ismael Soto and Phillip J. Haubrock are joint senior authors.

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1 | Introduction

Biological invasions refer to human-mediated introductions of organisms beyond their natural ranges and are major drivers of biodiversity loss, ecosystem disruption and economic damage worldwide (Ehrenfeld 2010; Roy et al. 2024). Through mechanisms such as competition, predation, parasitism, disease transmission, ecosystem engineering, and habitat alteration (Carneiro et al. 2025), non-native species can affect ecosystem functioning and services (Hulme 2009; Bell et al. 2021; Haubrock et al. 2026). Freshwater ecosystems are among the most threatened on the planet, harbouring high biodiversity, high endemism, and low functional redundancy, which make them particularly vulnerable to biological invasions (Strayer 2010; Havel et al. 2015; Dudgeon 2019). Non-native species threaten over a quarter of the world's freshwater fauna and have been implicated in the extinction of several others (Sayer et al. 2025). To date, there are at least 5000 reported aquatic non-native species globally (Briski et al. 2024), many of which have devastating ecological impacts (Twardochleb et al. 2013; Gallardo et al. 2016). Over 1500 of those are fish species, with 771 being freshwater fish (Haubrock et al. 2025a, 2025b).

Many non-native freshwater fishes were intentionally introduced (Gozlan et al. 2010; Cucherousset and Olden 2011; Hutchings 2014), aiming to improve freshwater fisheries (including sportfishing), enhance food security, or biologically control populations of unwanted organisms (Olden et al. 2022). However, some introduced non-native fishes cause substantial ecological disruption. For instance, the common carp (*Cyprinus carpio*) can significantly alter the physico-chemical properties and macrophyte communities of the invaded freshwater ecosystems (Vilizzi and Tarkan 2015; Collins 2025), while the Nile perch (*Lates niloticus*) has driven local extinctions of native fishes through predation and competition, decreasing biodiversity and altering habitats (Marshall 2018). In fact, the introduction of non-native freshwater fish species has been estimated to have caused an economic loss of at least US\$ 37.08 billion between 1960 and 2020 globally (Haubrock et al. 2022).

The magnitude of the impacts from non-native invasive freshwater fishes has made them the focus of multiple reviews, including the North American channel catfish (*Ictalurus punctatus*; Haubrock et al. 2022), goldfish (*Carassius auratus*; Massey et al. 2025), common carp (*Cyprinus carpio*; Vilizzi et al. 2015), and several members of the Poeciliidae and Cichlidae families (Stockwell and Henkanaththegedara 2011; Agostinho et al. 2021; Pritchard Cairns et al. 2024). Nevertheless, significant knowledge gaps persist regarding non-native freshwater fishes, leading to inefficient and often ineffective management strategies (Bernery et al. 2022). This is especially the case for the sunfish family (Centrarchidae), for which information on invasion ecology and history is limited, except for a few high-profile species, namely the largemouth bass (*Micropterus nigricans*; Takamura 2007; Costantini et al. 2023), pumpkinseed (*Lepomis gibbosus*; Cucherousset et al. 2009; Fox and Copp 2014), and smallmouth bass (*Micropterus dolomieu*; Carey et al. 2011; Loppnow et al. 2013). It is therefore critical to assess

their potential ecological, socio-economic, and cultural impacts to inform effective risk management. Recognizing this knowledge bias regarding non-native Centrarchidae (hereafter centrarchids), this scoping review provides the first comprehensive synthesis of: (i) the global taxonomic composition and known distribution of non-native centrarchids, (ii) their invasion pathways, vectors and impacts, (iii) potentially suitable areas and invasion risk and (iv) management approaches. This review aims to advance understanding of non-native centrarchid ecology and the risks they pose to native ecosystems.

2 | Methods

A scoping review was conducted using searches via platforms such as *Web of Science*, *Scopus* and *Google Scholar*, and consultations with experts. No explicit temporal restrictions were applied to the database searches and all records available in each platform from their inception until September 2025 were considered. This was complemented by conducting two literature searches. The first focused on studies of centrarchids within both their native and non-native ranges to obtain insights into research dynamics over time (Table S1). The second aimed to collate available information on risk screening and assessment of non-native centrarchids. Using the same scholarly databases, searches used combinations of keywords including species names (e.g., *Lepomis gibbosus*, *Micropterus salmoides*) and terms related to risk analysis, for example, 'risk identification', 'risk screening', 'risk assessment', 'Environmental Impact Classification for Alien Taxa' (EICAT), 'Socio-Economic Impact Classification of Alien Taxa' (SEICAT), 'Aquatic Species Invasiveness Screening Kit' (AS-ISK), 'Dispersal-Origin-Status-Impact' (DOSI). Both global and region-specific studies were considered.

2.1 | Non-Native Species Identification and Distribution

Non-native centrarchids were identified using the *Global Fish Invasion Database* (GFID; Haubrock et al. 2025b), the most comprehensive and up-to-date resource on established non-native fish species globally. The GFID encompasses records of 1535 established non-native fish species across 193 countries (5412 total occurrence records), supplemented by information on introduction pathways, habitat types, native biogeographic realms, impact types and mechanisms, and first record timelines. We identified the global distribution of non-native centrarchids at the country or state-level based on the scoping literature review, GFID data, and the *Nonindigenous Aquatic Species Database* (U.S. Geological Survey 2025). Specifically, we first identified countries or states outside their native range where centrarchids were reported (i.e., non-native), irrespective of establishment status, and then countries where they were reported as established. Additionally, we extracted occurrence information for all non-native centrarchids from the *Global Biodiversity Information Facility* (GBIF; GBIF.org 2025) via the *rgbif* R package (Chamberlain et al. 2022).

2.2 | Introduction Pathways

For each identified non-native Centrarchidae species, information on relevant pathways was extracted from GFID. This database compiles information based on Saul et al. (2017), following the standardized categorisation scheme adopted by the *Convention on Biological Diversity* (CBD 2014; Harrower et al. 2018), while also integrating information from the *Global Invasive Species Database* (GISD; Poorter and Browne 2005), *Delivering Alien Invasive Species Inventories for Europe* (DAISIE; Hulme et al. 2010), and the *European Alien Species Information Network* (EASIN; Katsanevakis et al. 2015). For each recorded pathway, information was structured into three key components: (1) the primary pathway category (following the CBD scheme: Release in nature, Escape from confinement, Transport—contaminant & stowaway, and Corridors); (2) a subcategory providing further detail on the specific mode of introduction (e.g., biological control, agriculture, aquaculture, ornamental purposes, ballast water transport; Saul et al. 2017); and (3) the intentionality of the introduction (i.e., whether the species was introduced in a given country on purpose [i.e., intentionally] or accidentally [i.e., unintentionally]; Table S2). We then tallied the number of species introduced per pathway and by intentionality. For species with multiple recorded pathways of introduction, each unique entry was counted individually. Therefore, if a non-native species was associated with two pathways of introduction (e.g., Release in nature and Escape from confinement), it was counted once per category. The same procedure was applied to the intentionality of introduction.

2.3 | Impacts

Information on impact types and mechanisms was derived from GFID. Impact information in GFID is based on the *Global Register of Introduced and Invasive Species* (GRIIS; Pagad et al. 2022), the *CABI Compendium* (CABI 2025), *FishBase* (www.fishbase.org; Froese and Paul 2025), and targeted internet searches. All searches were conducted in June 2025 using the combinations of listed keywords in Table S1. As such, it provides information on environmental/ecological (i.e., competition, disease transmission, hybridisation, interaction, predation, rapid [population] growth), social, and economic impact mechanisms. We counted the number of non-native Centrarchidae species associated with each impact mechanism. Species with multiple impact mechanisms were counted once per recorded mechanism.

2.4 | Impact and Risk Assessment/Screening

From the conducted systematic literature search, we extracted information on risk screening and assessment conducted for non-native centrarchids. We also recorded all information available for each species in different regions to capture context-dependence in invasion potential. We then tabulated these data from published studies across multiple regions (Table S3). From AS-ISK studies, we extracted all available risk scores (i.e., Basic Risk Assessment (BRA) and Climate Change Assessment (CCA)), global invasiveness thresholds, and categorical classifications. This enabled comparisons across taxa and geographic

areas and the identification of consistencies and regional contrasts in invasion risk.

2.5 | Species Distribution Modelling

To identify the potential distribution of all known non-native Centrarchidae species and selected species-specific examples, we developed a series of Species Distribution Models (SDMs). First, we compiled species occurrence records from GBIF at the global scale. Occurrences were cleaned using the *CoordinateCleaner* R package (Zizka et al. 2019) to flag potential erroneous entries (e.g., occurrences labelled as preserved specimens or fossil records) for removal. Climatic, environmental, and socio-economic predictors were included to model the distribution of non-native centrarchids. These included: elevation, distance to major cities, terrain roughness (Amatulli et al. 2018) and gridded Gross Domestic Product (Wang and Sun 2023). Bioclimatic predictors were extracted from the CHELSA database (Karger et al. 2023). Each predictor was standardized at a resolution of 0.083 (approx. 9.25 km × 9.25 km). Multicollinearity was assessed with the *vifstep* function from the *usdm* R package (Naimi et al. 2014), which iteratively removed the highest correlated predictor based on Variance Inflation Factor (VIF). Only predictors with VIF < 5 were retained. SDMs were implemented using the *sdm* R package (Naimi and Araújo 2016). For all SDMs, occurrences were compared with 10,000 background points randomly sampled. Species-environment relationships were modelled using three common algorithms: generalized linear models (GLMs), boosted regression trees (BRTs) and BIOCLIM. Models were evaluated using subsampling and bootstrapping methods with three iterations and a 30% test data split. Predictive performance for each model was assessed using the area under the receiver operating curve (AUC) and combined into a weighted ensemble model using the AUC (Table S4). Consequently, we combined the SDMs of each species by summing the values of each cell and standardized them from 0 (low) to 1 (high suitability).

3 | Results

In total, 309 primary sources were scanned for their relevance, with 217 considered relevant for this review on non-native centrarchids (Data S1). General research on centrarchids started 30 years before non-native centrarchids were contextualized and also increased more steeply to the extent that there were 304 articles published in 2024 on native centrarchids versus 60 on non-native centrarchids (Figure 1).

3.1 | Taxonomic and Ecological Overview

The Centrarchidae family comprises freshwater ray-finned fishes endemic to North America that were previously classified within the order Perciformes but recently assigned to the independent order Centrarchiformes (Betancur-R et al. 2013; Near et al. 2013). “Centrarchidae” is derived from a distinctive morphological trait shared by its members: the presence of robust spines in the anal fin (Warren Jr. 2009). Currently, this family comprises 41 living recognized species across eight

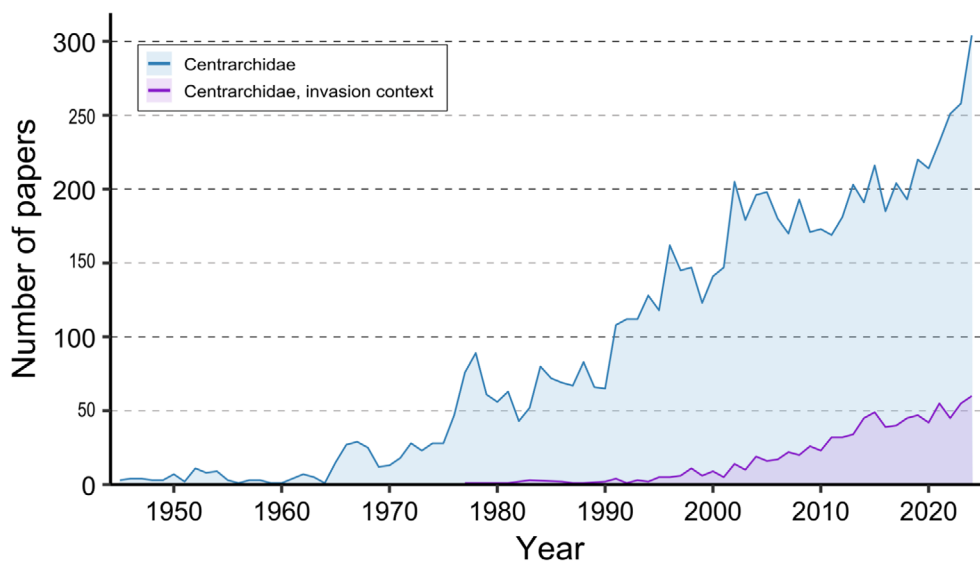


FIGURE 1 | Temporal trends in peer-reviewed publications on Centrarchidae in general (blue) and in the context of biological invasions (purple).

genera (Fricke et al. 2025), making it one of the most species-rich freshwater fish families endemic to North America (Warren Jr. 2009). Phylogenetically, centrarchids are divided into several major clades, including the subfamily Lepominae containing genera of *Lepomis* (true sunfishes) and *Micropterus* (black basses), as well as the subfamily Centrarchinae, which comprises six distinct genera: *Pomoxis* (crappies), *Enneacanthus*, *Centrarchus*, *Ambloplites*, *Archoplites* and *Acantharchus* (Near and Kim 2021). Importantly, Centrarchidae taxonomy continues to undergo revision as molecular phylogenetics and population-level genetic studies refine species boundaries (Kim et al. 2022; Fricke et al. 2025; Figure 2).

Centrarchids occupy freshwater ecosystems, although some species can tolerate moderate salinity (Near and Koppelman 2009). They typically inhabit warm lentic environments and low- to mid-order rivers, with preferences for littoral zones with abundant submerged vegetation, woody debris, or rocky substrates that provide habitats for foraging, refuge, and nesting (Page and Burr 2011). Because centrarchids are warmwater fishes, their natural distribution is primarily limited northward by thermal constraints, so they are present from northern Mexico up to and including parts of southern Canada. Their native distribution is largely restricted to areas east of the Rocky Mountains, except the Sacramento perch (*A. interruptus*) that is native to California's Central Valley (Warren Jr. 2009; Crain and Moyle 2011). Seven centrarchids occur naturally in southern Canada—bluegill (*L. macrochirus*), green sunfish (*L. cyanellus*), Northern sunfish (*L. peltastes*), pumpkinseed (*L. gibbosus*), redbreast sunfish (*L. auritus*), rock bass (*A. rupestris*), smallmouth bass (*M. dolomieu*) and three in Mexico, Plains longear sunfish (*L. aquilensis*), bluegill (*L. macrochirus*), and largemouth bass (*M. nigricans*) (Fricke et al. 2025; Figure 3).

As opportunistic foragers, centrarchid diets are diverse, consuming a wide range of organisms, depending on their availability. Like many freshwater fish, juveniles initially prey

on zooplankton, with ontogenetic shifts towards larger prey (Section 3.4). Broadly speaking, most centrarchids can be considered dietary generalists, consuming zooplankton, insect larvae, crustaceans, molluscs, fish, amphibians and aquatic and terrestrial insects, with prey items dependent on centrarchid size and life stage (Bosman 2003; Almeida et al. 2012; Cárdenas-Mahecha et al. 2022). However, it is important to note that diversification within the most species-rich centrarchid genera, particularly *Lepomis*, has been driven in part by trophic specialisation and diverging jaw morphology (e.g., mollusc-crushing pumpkinseed versus zooplanktivorous bluegill), including pelagic-littoral ecomorph differentiation, which is directly relevant for assessing competitive interactions and invasion risk (Wainwright et al. 1991; Robinson et al. 1993). Finally, centrarchids are iteroparous batch spawners with external fertilisation and male parental care (Brown 1984). Water temperature drives reproductive phenology in lakes (Shuter and Post 1990) and rivers (Rubenson and Olden 2016), typically occurring when water reaches $\sim 14^{\circ}\text{C}$ – 26°C (Cooke et al. 2010).

3.2 | Distribution of Non-Native Centrarchidae

3.2.1 | Overview

At least seven of the eight genera of the centrarchid family—*Ambloplites*, *Archoplites*, *Centrarchus*, *Enneacanthus*, *Lepomis*, *Micropterus* and *Pomoxis*—include at least one reported species introduced beyond its native range (the only exception being the *Acantharchus* genus; Haubrock et al. 2025b). The socio-economic importance of centrarchids is the main reason for introductions across the globe (Gozlan et al. 2010), with introductions for sportfishing, aquaculture and ornamental purposes (Hargrove et al. 2015; Patoka et al. 2017; Li et al. 2025). Centrarchids are now present on all continents, except Antarctica (Table 1), with 14 species being considered “invasive” in several countries (Table S5) and ecological impacts ranging from the individual to ecosystem level (see Section 3.5 below).

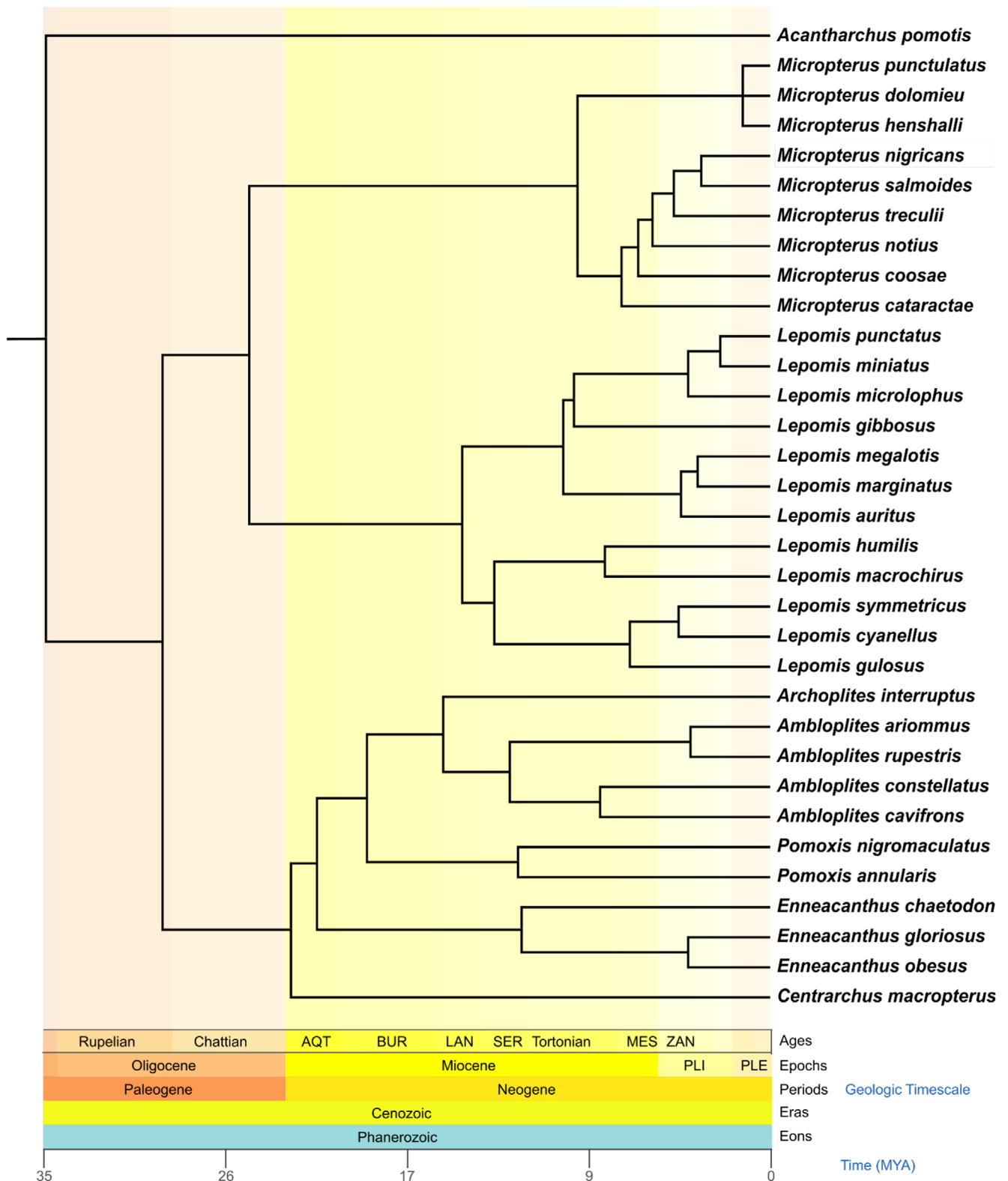


FIGURE 2 | Evolutionary tree of 33 Centrarchidae species based on divergence times. Branch lengths show estimated time since species split, measured in millions of years (modified from Kumar et al. 2022).

3.2.2 | North American Distribution of Non-Native Centrarchids

While the native range of centrarchids includes most of North America—including the majority of the United States of America

and parts of Canada and northern Mexico—their regional distribution varies across species (Near and Koppelman 2009). In North America, translocations of centrarchids date back to the early 19th century, when these species were moved to support fisheries. Such translocations were widespread but poorly documented, and in

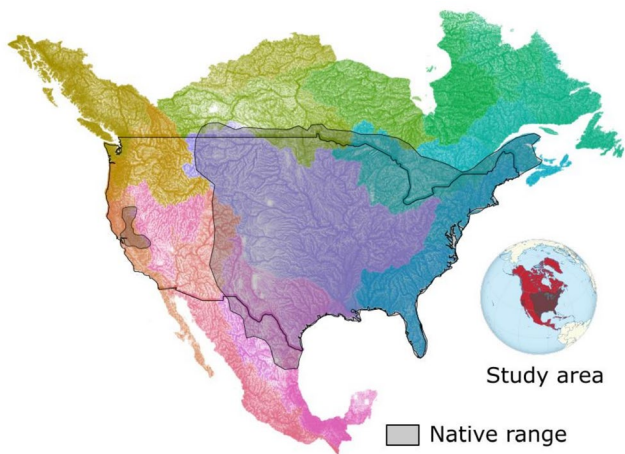


FIGURE 3 | Part of North America, where the shaded area represents the native range of the Centrarchidae family (based on Soes et al. 2010), and national borders are represented by black lines. Different colours represent hydrological basins where river size is scaled based on Strahler order. Basins and rivers were obtained from HydroSHEDS (www.hydrosheds.org; Lehner and Grill 2013). The national borders of the United States of America (excluding Alaska) are outlined in black.

TABLE 1 | Number of invaded countries and reported non-native Centrarchidae by continent according to the *Global Fish Invasion Database* (GFID; Haubrock et al. 2025b).

Continent	Number of countries reporting non-native Centrarchidae species	Reported number of non-native Centrarchidae species
Africa	22	9
Asia	13	9
Europe	34	10
North America ^a	12	30
Oceania	4	1
South America	7	4

^aNote that translocations within North America and the United States of America are described in Section 3.2.2.

some cases not recorded at all (Nico and Fuller 1999). Moreover, during this period of early introductions, taxonomic work was less developed, and molecular methods were entirely lacking, leading to dubious records (Kim et al. 2024).

All known Centrarchidae species established outside North America ($n = 30$) have also established populations beyond their native ranges within their countries of origin. Within the genus *Lepomis*, 11 species have extensive non-native ranges across North America (Figure 4), including the green sunfish (*L. cyanellus*), bluegill (*L. macrochirus*), redear sunfish (*L. microlophus*), warmouth (*L. gulosus*) and pumpkinseed (*L. gibbosus*) (Fuller and Cannister 2025a, 2025b; Fuller et al. 2025a, 2025b). The non-native ranges of these species are not confined to areas

contiguous with their native distributions but extend into more distant and isolated regions. In contrast, species such as the longear sunfish (*L. megalotis*), orange spotted sunfish (*L. humilis*), redspotted sunfish (*L. miniatus*) and redbreast sunfish (*L. auritus*) exhibit more restricted non-native distributions, primarily limited to areas adjacent to their native ranges (Fuller and Cannister 2025c, 2025d, 2025e; Fuller et al. 2025c). Largemouth bass (*M. nigricans*) and smallmouth bass (*M. dolomieu*) are the most widespread non-native species of the genus, extending across nearly all of the contiguous United States of America and into southern Canada (Fuller et al. 2025d, 2025e). The seven remaining species of the genus that have non-native populations in North America exhibit far more limited distributions. Most of these species have smaller non-native ranges, and their introduced populations are largely confined to areas adjacent to their native distributions. These species include the redeye bass (*M. coosae*), shoal bass (*M. cataractae*), Alabama bass (*M. henshalli*) and Guadalupe bass (*M. treculii*) (Benson 2025; Fuller 2025a, 2025b, 2025c). The spotted bass (*M. punctulatus*) has a relatively broader non-native distribution but still does not match the extent of largemouth bass (*M. nigricans*) or smallmouth bass (*M. dolomieu*) (Fuller et al. 2025f). Within the genus *Ambloplites*, the most widespread is rock bass (*A. rupestris*), whereas the other two species, the Ozark bass (*A. constellatus*) and Roanoke bass (*A. cavifrons*), have more limited non-native ranges, concentrated in the central and eastern United States, respectively (Figure 4; Fuller 2025d, 2025e; Fuller and Neilson 2025). Both *Pomoxis* species, the black crappie (*P. nigromaculatus*) and white crappie (*P. annularis*), exhibit extensive non-native distribution across the United States of America (Fuller et al. 2025g, 2025h).

3.2.3 | Global Distribution of Non-Native Centrarchidae

There are 30 species of centrarchids that are non-native across all continents except Antarctica (Table 2, Figure 5). The genus *Lepomis* contains the highest number of non-native species ($n = 11$ species), followed by *Micropterus* ($n = 9$), *Ambloplites* ($n = 4$), *Pomoxis* ($n = 2$), *Enneacanthus* ($n = 2$), *Archoplites* ($n = 1$) and *Centrarchus* ($n = 1$). When North America is excluded from this analysis, 17 centrarchids are reported with established non-native populations, including eight species of the genus *Lepomis*, five of the genus *Micropterus*, two of the genus *Pomoxis*, and one species each of *Ambloplites* and *Enneacanthus*.

Overall, the largemouth bass (*M. nigricans*) is the most widely reported member of the family Centrarchidae introduced beyond its native range, with introductions reported in at least 77 countries worldwide (Long and Seguy 2024; Haubrock et al. 2025a). In many of these countries, it is regarded as invasive (i.e., by causing impacts and/or spreading; *sensu* Soto et al. 2024), making it one of the most extensively studied non-native Centrarchidae species globally (Long and Seguy 2024; Haubrock et al. 2025b). The pumpkinseed (*L. gibbosus*) ranks second, having been introduced to at least 44 countries. Other species such as the bluegill (*L. macrochirus*; $n \geq 23$ countries), smallmouth bass (*M. dolomieu*; $n \geq 17$), and green sunfish (*L. cyanellus*; $n \geq 16$) have been introduced into more than 10 countries, while redear sunfish (*L. microlophus*; $n \geq 7$), redbreast sunfish (*L. auritus*; $n \geq 7$), black crappie (*P. nigromaculatus*; $n \geq 7$), warmouth (*L. gulosus*; $n \geq 4$), rock bass (*A. rupestris*; $n \geq 4$) and white crappie (*P. annularis*; $n \geq 4$) have been introduced

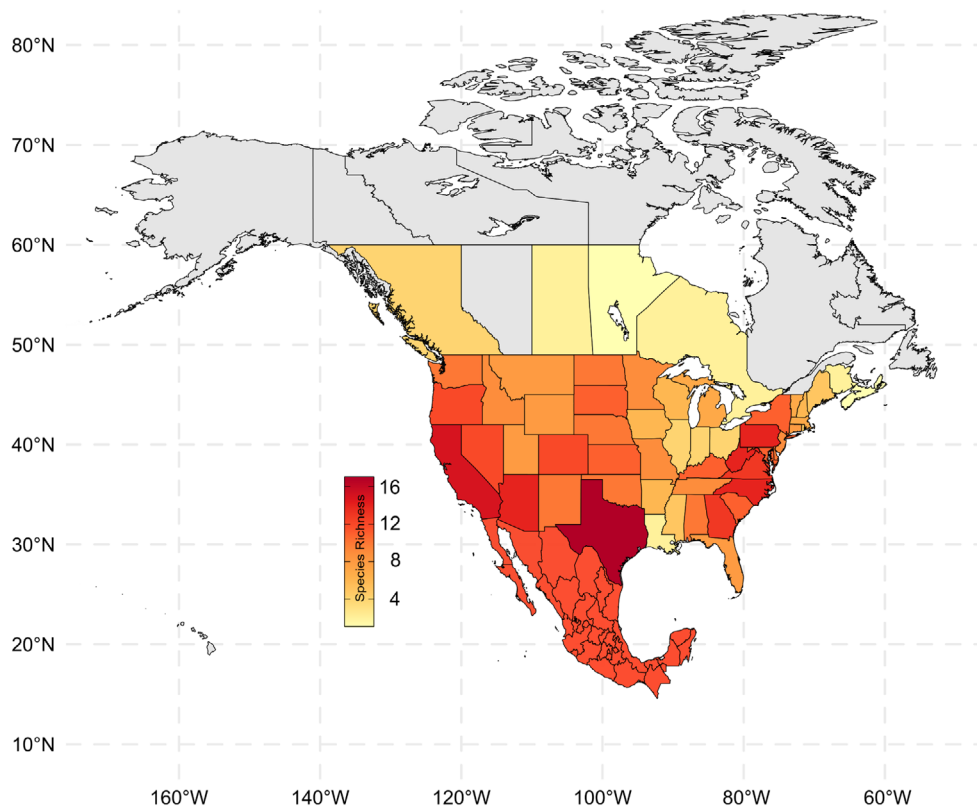


FIGURE 4 | Non-native Centrarchidae species distribution in North America. Data represent species that have been introduced into freshwater ecosystems outside their native range, including areas adjacent to their original distribution (Data extracted from the *Nonindigenous Aquatic Species Database*) (U.S. Geological Survey 2025).

to comparably fewer countries. However, some species have been introduced more frequently within particular continents. For example, pumpkinseed (*L. gibbosus*) is especially common in Europe (García-Berthou et al. 2005), whereas bluegill (*L. macrochirus*) and green sunfish (*L. cyanellus*) are more widespread in Africa. See Data S2 for a more detailed description of selected species of centrarchids.

Most other species have been reported in very few countries. However, taxonomic revisions have added complexity to interpreting non-native records. Historically, *M. salmoides* was widely reported as the primary introduced largemouth bass species but recent genomic and taxonomic work (Kim et al. 2022) reviewed the taxonomy of the *Micropterus* genus, revealing that *M. salmoides* should be applied to the species known as the Florida bass (previously *M. floridanus* or *M. salmoides floridanus*) and *M. nigricans* should be applied to the largemouth bass, which is the species introduced worldwide—including in Europe, Asia and Africa (e.g., García-Berthou et al. 2005; iNaturalist 2025). While *M. salmoides* is still considered valid and appears to be established in parts of Japan, South Africa, and some regions of the United States of America where it was introduced (e.g., Texas and Virginia), most records historically labelled as *M. salmoides* in non-native areas are now assumed to be *M. nigricans* unless confirmed otherwise (see Section 3.2.3). Moreover, hybridisation between *M. salmoides* and *M. nigricans* has been documented in several regions, including the United States of America and Japan (Qin 2024; Fricke et al. 2025), complicating species identification and the tracking of introduced lineages (Kim et al. 2022).

Regarding species richness, Europe ($n=10$ species) hosts the greatest number of established non-native Centrarchidae species, followed by Asia and Africa ($n=9$ each), South America ($n=4$) and Oceania ($n=1$). Within Europe, Germany and Norway record the highest number of established centrarchids ($n=6$ each), followed by France ($n=4$), and Italy, Austria, Belgium, and the United Kingdom ($n=3$ each), with other countries hosting fewer species. In Asia, China records the greatest number of introduced species ($n=6$), followed by Japan ($n=4$) and the Philippines ($n=3$). In Africa, the highest number of species is recorded in South Africa ($n=7$), followed by Eswatini, Zambia and Zimbabwe ($n=6$ each), with other African countries hosting five species or less. In South America, Brazil has the highest record ($n=4$), followed by Venezuela ($n=2$), while Argentina, Bolivia, Colombia, and Ecuador have one record each. In Oceania, Fiji, Guam, Micronesia, New Caledonia each hold one record (*M. nigricans*) (Figure 5).

3.3 | Introduction Pathways and Factors Affecting Establishment

3.3.1 | Pathways

Within the overall native range of Centrarchidae species (Figure 6), many non-native populations established following introductions via recreational fisheries (Carey et al. 2011; Hartman and Larson 2023; Dean et al. 2024). Indeed, at the national scale, the majority of recorded non-native Centrarchidae species introductions have been classified as intentional

TABLE 2 | List of known non-native Centrarchidae species (excluding hybrids) and the countries where they have been reported as non-native based on the *Global Fish Invasion Database* (GFID; Haubrock et al. 2025b), relevant literature sources and knowledge of the authors.

Genus	Species	Common name	Presence
<i>Ambloplites</i>	<i>Ambloplites ariommus</i>	Shadow bass	United States of America
	<i>Ambloplites cavifrons</i>	Roanoke bass	United States of America
	<i>Ambloplites constellatus</i>	Ozark bass	United States of America
	<i>Ambloplites rupestris</i>	Rock bass	France, Mexico, United Kingdom, United States of America
<i>Archoplites</i>	<i>Archoplites interruptus</i>	Sacramento perch	United States of America
<i>Centrarchus</i>	<i>Centrarchus macropterus</i>	Flier	United States of America
<i>Enneacanthus</i>	<i>Enneacanthus gloriosus</i>	Blue-spotted sunfish	Canada, United States of America
	<i>Enneacanthus obesus</i>	Banded sunfish	Germany, United States of America
<i>Lepomis</i>	<i>Lepomis auritus</i>	Redbreast sunfish	China, Dominican Republic, Germany, Italy, Mexico, Puerto Rico, United States of America
	<i>Lepomis cyanellus</i>	Green sunfish	Brazil, China, Congo, Eswatini, Kenya, Madagascar, Mauritius, Mexico, Morocco, Norway, Philippines, South Africa, United States of America, Zambia, Zimbabwe
	<i>Lepomis gibbosus</i>	Pumpkinseed	Albania, Austria, Belarus, Belgium, Bosnia and Herzegovina, Brazil, Bulgaria, Canada, Chile, Congo, Croatia, Cuba, Cyprus, Czechia, Denmark, France, Georgia, Germany, Greece, Guatemala, Hungary, Italy, Luxembourg, Moldova, Montenegro, Morocco, Netherlands, North Macedonia, Norway, Poland, Portugal, Romania, Russia, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Türkiye, Ukraine, United Kingdom, United States of America, Venezuela
	<i>Lepomis gulosus</i>	Warmouth	Canada, Mexico, Puerto Rico, United States of America
	<i>Lepomis humilis</i>	Orangespotted sunfish	Canada, United States of America
	<i>Lepomis macrochirus</i>	Bluegill	Brazil, China, Cuba, Democratic Republic of Congo, El Salvador, Eswatini, Iran, Japan, Kenya, Madagascar, Malawi, Mauritius, Morocco, Panama, Philippines, Puerto Rico, South Africa, South Korea, United States of America, Venezuela, Zambia, Zimbabwe
	<i>Lepomis marginatus</i>	Dollar sunfish	Mexico
	<i>Lepomis megalotis</i>	Longear sunfish	China, Germany, Mexico, United States of America
	<i>Lepomis microlophus</i>	Redear sunfish	Canada, Mauritius, Mexico, Morocco, Panama, Puerto Rico, United States of America
	<i>Lepomis miniatus</i>	Redspotted sunfish	United States of America
	<i>Lepomis punctatus</i>	Spotted sunfish	Eswatini, Mexico, South Africa, Zambia, Zimbabwe

(Continues)

($n=206$) (Figure 6a), while the main pathway of introduction was classified as ‘Escape from confinement’ ($n=188$ species), followed by ‘Unknown’ ($n=19$) and “Release in nature” ($n=18$) (Figure 6b). Among the subcategories under ‘Escape from confinement’, ‘Aquaculture’ ($n=184$) is the dominant mechanism

responsible for the introduction of non-native centrarchids, with “Ornamental” ($n=4$) making only a small contribution (Figure 6c). Among subcategories under ‘Release in nature’, ‘Fishery in the wild’ ($n=11$) was reported more frequently than ‘Biological control’ ($n=7$) (Figure 6c). Given that pathways are

TABLE 2 | (Continued)

Genus	Species	Common name	Presence
<i>Micropterus</i>	<i>Micropterus cataractae</i>	Shoal bass	United States of America
	<i>Micropterus coosae</i>	Redeye bass	Puerto Rico, United States of America
	<i>Micropterus dolomieu</i>	Smallmouth bass	Austria, Belgium, Belize, Canada, Eswatini, Germany, Japan, Mauritius, Mexico, Norway, South Africa, Tanzania, United States of America, Vietnam, Sweden, Zambia, Zimbabwe
	<i>Micropterus henshalli</i>	Alabama bass	United States of America
	<i>Micropterus nigricans</i> (formerly <i>M. salmoides</i>)	Largemouth bass	Argentina, Austria, Belgium, Bolivia, Bosnia and Herzegovina, Botswana, Brazil, Cameroon, Canada, China, Colombia, Congo, Costa Rica, Croatia, Cuba, Cyprus, Czechia, Democratic Republic of Congo, Denmark, Dominican Republic, Ecuador, El Salvador, Eswatini, Fiji, Finland, France, Germany, Greece, Guam, Guatemala, Honduras, Hungary, Indonesia, Iran, Italy, Japan, Kenya, Lesotho, Madagascar, Malawi, Malaysia, Mauritius, Mexico, Micronesia, Morocco, Mozambique, Namibia, Netherlands, New Caledonia, Nigeria, North Korea, Norway, Panama, Philippines, Poland, Portugal, Puerto Rico, Russia, Serbia, Slovakia, Slovenia, South Africa, South Korea, Spain, Sweden, Switzerland, Taiwan, Tanzania, Tunisia, Uganda, Ukraine, United Kingdom, United States of America, Vietnam, Zambia, Zimbabwe
	<i>Micropterus notius</i>	Suwannee bass	United States of America
	<i>Micropterus punctulatus</i>	Spotted bass	Eswatini, South Africa, United States of America, Zambia, Zimbabwe
	<i>Micropterus salmoides</i> (formerly <i>M. floridanus</i> or <i>M. salmoides floridanus</i>)	Florida bass	Japan, South Africa, United States of America
	<i>Micropterus treculii</i>	Guadalupe bass	United States of America
	<i>Pomoxis annularis</i>	White crappie	Mexico, Norway, Panama, United States of America
<i>Pomoxis</i>	<i>Pomoxis nigromaculatus</i>	Black crappie	Canada, China, France, Mexico, Norway, Panama, United States of America,

Note: Not all species have established populations in the countries where they have been reported. See Data S2 for a detailed portrayal of selected species.

unknown for many centrarchids and that unintentional freshwater fish introductions (e.g., via ballast water or contaminated stocks) are comparatively rare, non-native spread in this family is more plausibly driven by unreported but intentional releases, such as unauthorized sport stocking or pet trade introductions (Ishikawa and Tachihara 2014; Banha et al. 2024).

Centrarchidae species are mostly valued for their socio-economic benefits (Embke et al. 2022). Similar to most of the non-native fish species established outside their native ranges, Centrarchidae species are highly valued in aquaculture, one of the leading introduction pathways for non-native freshwater fish species globally (Haubrock et al. 2025a; Oficialdegui et al. 2025). For example, largemouth bass (*M. nigricans*)—valued for its meat quality—is a major aquaculture product in China and is produced in over 90% of its mainland provinces (Fang et al. 2023). Although introductions through ornamental trade are not commonly reported, some

of the most widely distributed centrarchids, such as pumpkinseed (*L. gibbosus*) and blackbanded sunfish (*E. chaetodon*), have been introduced through this pathway, presumably due to their colourful appearance and attractiveness (Maceda-Veiga et al. 2013; Lipták et al. 2023). The perception of these species as lucrative commodities further complicates non-native species introduction dynamics, with countries establishing hatcheries to cater to demand, inadvertently increasing propagule pressure and the likelihood of establishment (Consuegra et al. 2011).

The popularity of several Centrarchidae species as sportfishes has facilitated their continued introduction in several countries, such as France (Cucherousset et al. 2021) and South Africa (Hargrove et al. 2017), as a result of stocking efforts to support or establish recreational fisheries. Other Centrarchidae species, such as green sunfish (*L. cyanellus*) and redear sunfish (*L. microlophus*), have been introduced as biocontrol agents for mosquito larvae and

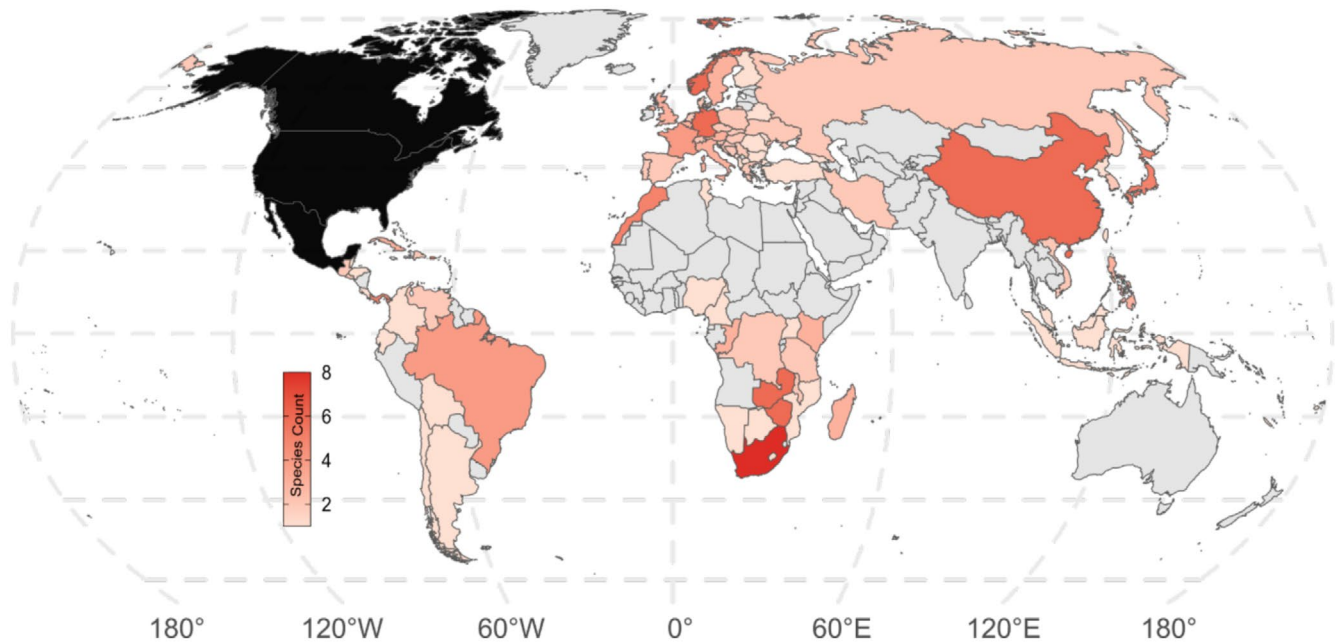


FIGURE 5 | The number of non-native Centrarchidae species per country based on the *Global Fish Invasion Database* (GFID; Haubrock et al. 2025b). See Figure S1 for an overview of reported occurrences in the *Global Biodiversity Information Facility* (GBIF). Translocations within North America (Canada, United States of America and Mexico; see Figure 3); countries coloured in black are not considered.

snails, although often with questionable outcomes (Downs 1991; Ledford and Kelly 2006; Tsunoda and Mitsuo 2012). Largemouth bass (*M. nigricans*) was also introduced to control bluegill (*L. macrochirus*) in Japanese ponds, in an attempt to enhance populations of Japanese white crucian carp (*Carassius cuvieri*), which, besides being ineffective, also resulted in decreased abundance of other native species (Azuma and Motomura 1998).

3.3.2 | Factors Affecting Establishment

Following introduction, the ability of non-native species to become invasive requires the establishment of sustainable populations, a process determined by propagule pressure and biological resistance from the recipient ecosystem among other factors (Thomaz 2022). However, the abiotic conditions of the receiving environment are also key factors in the ability of these fish to reproduce and then recruit. In lakes, climate is hypothesized to control the upper latitudinal distribution of centrarchids due to increasing overwinter mortality of juveniles (Shuter and Post 1990). The summer growing season for young-of-year bass must be of sufficient duration to reach a critical minimum size. Otherwise, the probability of mortality from overwinter starvation increases, as smaller fish have a lower capacity to store energy relative to larger individuals. The critical size required for overwinter survival varies with species and winter duration (Shuter et al. 1980). With increasing northern latitude, the combination of winter duration and shortened growing season reduces overwinter survival of young-of-year *Micropterus* spp. Size-dependent overwinter survival in smallmouth bass (*M. dolomieu*) has been demonstrated in both field and laboratory studies (Curry et al. 2005). At lower latitudes, researchers have also suggested that attaining a critical size is important for reducing young-of-year largemouth bass (*M. nigricans*) susceptibility to predation (Suski and Ridgway 2009).

In rivers, strong thermal gradients, transitioning from warmer, longer summers downstream to colder, shorter summers upstream play an important role in shaping the longitudinal distribution of smallmouth bass (*M. dolomieu*) (Rubenson and Olden 2020). Strong gradients in thermal regimes have been shown to control the upstream extent of bass populations in rivers, because their young-of-year are confronted by reduced growth potential and increasingly severe winters as they move upstream (Lawrence et al. 2012, 2015). Additionally, high-gradient reaches limit their upstream expansion by serving as barriers to movement, especially during high flows. For example, smallmouth bass (*M. dolomieu*) rarely occupy areas with gradients exceeding 10m km^{-1} in its native range (Brewer et al. 2007; Dauwalter et al. 2007), and 8m km^{-1} in its introduced range (Lawrence et al. 2012). Similarly, the distribution of largemouth bass (*M. nigricans*) in the Iberian Peninsula has been shown to mostly depend on temperature, with this invasive species being more prevalent in the mainstem of rivers and at southern latitudes (Bae et al. 2018). Moreover, successful establishment may depend on oxygen availability because its depletion during prolonged ice cover can trigger winterkills that selectively eliminate sensitive centrarchids such as *Micropterus* spp., while more tolerant species like pumpkinseed (*L. gibbosus*) often persist, thereby shaping invasion success in shallow, nutrient-rich systems (Schofield et al. 2007; Hasler et al. 2009; Suski and Ridgway 2009).

3.4 | Traits and Genetic Characteristics of Non-Native Centrarchids

3.4.1 | Traits of Non-Native Centrarchids

Several morphological and behavioural traits of non-native Centrarchidae species (Table 3) contribute to their ability to establish and integrate into native food webs by successfully competing

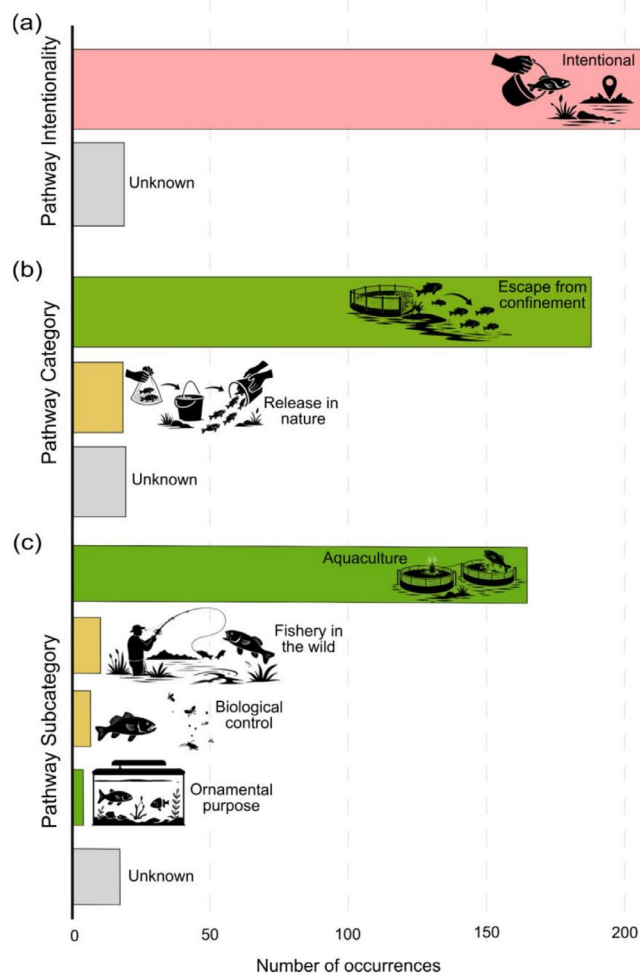


FIGURE 6 | Occurrences of introduction pathways for non-native Centrarchidae species broken down by (a) intentionality of introductions, (b) pathways category and (c) pathways subcategory based on the *Global Fish Invasion Database* (Haubrock et al. 2025b).

for resources (Godinho and Ferreira 2014; Moran et al. 2018). A key trait is opportunistic feeding, which allows centrarchids to adjust their diet according to the most prevalent prey in invaded ecosystems, facilitating their establishment across diverse habitats (Godinho and Ferreira 2014; García-Berthou 2002). Although centrarchids tend to be generalists in their foraging, and many species occupy high trophic positions, interspecific differences are also apparent. Most *Micropterus* species are apex predators, feeding opportunistically on fish and invertebrates (including crayfish) (Huskey and Turingan 2001; García-Berthou 2002; Wheeler and Allen 2003; Warren Jr. 2009), with evidence that these species can feed on terrestrial vertebrates (e.g., amphibians, reptiles, birds) (Hodgson and Hansen 2005). Large adult body size is also advantageous, as it broadens the available prey spectrum and reduces predation risk (Costantini et al. 2023). *Lepomis* species usually occupy an intermediate trophic position (i.e., mesopredators), preying on invertebrates and small fishes (Flemer and Woolcott 1966; Mittelbach et al. 1992; García-Berthou and Moreno-Amich 2000; Olson et al. 2003; Warren Jr. 2009). Species of the genus *Ambloplites*—rock bass (*A. rupestris*), shadow bass (*A. ariommus*) and Roanoke bass (*A. cavifrons*)—are primarily benthic feeders, with larger invertebrates constituting the main component of their diets (McBride et al. 1982; Probst et al. 1984; Warren Jr. 2009). The

white crappie (*P. annularis*), however, is primarily a particulate-feeding zooplanktivore and invertivore (Mathur and Robbins 1971; Mathur 1972; Browman and O'Brien 1995), and the black crappie (*P. nigromaculatus*) is considered a midwater invertivore (Warren Jr. 2009).

Centrarchids tend to have relatively long lifespans (Table 3), which enables multiple reproductive events during an individual's life (Marchetti et al. 2004; Bernery et al. 2023). The lifespan of largemouth bass (*M. nigricans*) has been recorded up to 14 years in non-native regions, although individuals rarely live longer than 9 years (Costantini et al. 2023). Non-native centrarchids tend to be highly fecund (Copp and Fox 2007; Costantini et al. 2023) and exhibit similar reproductive behaviours that involve males constructing and guarding nests (Gross and Charnov 1980; Neff 2003; Cooke et al. 2008), which generally results in high offspring survival (Costantini et al. 2023). Nest defence duration, behaviour and associated attack distances are species-specific (Colgan and Brown 1988). While rock bass (*A. rupestris*) typically ceases parental care once the fry leave the nest, largemouth bass (*M. nigricans*) guards progeny for up to a month (Brown 1984). Within species, both colonial and solitary nesting behaviours can be expressed (Neff et al. 2004). Centrarchids also benefit from enemy release, with few natural, co-evolved predators and a relative tolerance to many parasites in their invaded ranges (Ondračková, Fojtů, et al. 2019; Ondračková, Kvach, et al. 2019; Dudliv et al. 2024). Many centrarchids are eurythermal and tolerant to suboptimal water quality, enabling persistence in degraded or heavily modified habitats. For example, largemouth bass (*M. nigricans*) tolerate a broad temperature range (0.1°C–39.4°C) and can inhabit both fresh and brackish waters (Costantini et al. 2023). Some *Lepomis* species can tolerate a wide range of hypoxic conditions (Smale and Rabeni 1995; Marchetti et al. 2004; Farwell et al. 2007).

Centrarchids also tend to have high aesthetic appeal (Table 3), which is a key driver of their introductions (Holčík 1991). This appeal stems from their colourful appearance (making them very popular in the aquarium trade; Patoka et al. 2017), and behavioural complexity, aggression, and size that make them attractive for sport fisheries, such as the largemouth bass (*M. nigricans*) and smallmouth bass (*M. dolomieu*) (Long and Seguy 2024).

3.4.2 | Genetic Characteristics of Introduced Centrarchid Populations

Many established populations of centrarchids exhibit low genetic diversity relative to native populations, which is consistent with genetic bottlenecks stemming from founder effects (Lau et al. 2009; Kvach et al. 2024). For example, pumpkinseed (*L. gibbosus*) shows reduced genetic variability in introduced populations in southwestern Europe (Yavno et al. 2020; Lambea-Cambor et al. 2023) and Türkiye (Keskin et al. 2013; Ağdamar et al. 2015). Bhagat et al. (2011) examined patterns of genetic diversity and differentiation among pumpkinseed (*L. gibbosus*) in Portugal and identified two distinct genetic groups among eight reservoir populations, indicating at least two colonisation events. Significantly reduced genetic diversity among introduced populations of largemouth bass (*M. nigricans*) has been documented across its non-native range, including China (Bai

TABLE 3 | Examples of traits that benefit the invasiveness of non-native Centrarchidae.

Trait	Invasion stage	Why it aids invasion	Example species	References
Colourful appearance	Transport and introduction	Attractive colouration makes species popular in the aquarium and pet trade, promoting human-mediated transport.	<i>L. gibbosus</i>	Patoka et al. (2017)
Good meat quality	Transport and introduction	Valued for aquaculture and consumption, leading to intentional or non-intentional introductions by humans.	<i>M. nigricans</i>	Fang et al. (2023)
Nest building and parental care	Establishment	Enhances offspring survival and promotes successful population establishment.	<i>M. nigricans</i>	Costantini et al. (2023); Bernery et al. (2023)
Dietary opportunism	Establishment	Opportunistic feeding behaviour allows for easier establishment	<i>M. nigricans</i> , <i>L. gibbosus</i>	Godinho and Ferreira (2014)
Tolerance to suboptimal conditions	Transport, Establishment	Allows survival and reproduction across a wide range of environmental conditions.	<i>M. nigricans</i> , <i>L. gibbosus</i> , <i>L. humilis</i> , <i>L. cyanellus</i> , <i>L. macrochirus</i> , <i>L. megalotis</i>	Smale and Rabeni (1995); Farwell et al. (2007); Costantini et al. (2023)
High fecundity	Spread, Impact	Produces large numbers of offspring, enabling rapid population growth and dispersal.	<i>L. gibbosus</i> , <i>M. nigricans</i>	Copp and Fox (2007) Costantini et al. (2023)
Fast maturation	Spread	Short generation time facilitates quick population turnover and spread.	<i>L. gibbosus</i>	Fox and Copp (2014)
Relative resistance to parasites	Impact	Can act as parasite reservoirs, negatively affecting native species through disease transmission.	<i>L. gibbosus</i>	Tkachenko et al. (2025)
Long lifespan	Impact	Long-lived individuals can maintain ecological pressure on native communities over extended periods.	<i>M. nigricans</i>	Costantini et al. (2023)

et al. 2008), Brazil (Frehe et al. 2020), South Africa (Hargrove et al. 2017), and Japan (Yokogawa 1998). In South Africa, 88 individuals of largemouth bass (*M. nigricans*) were introduced in 1928 via two shipments of fingerlings distributed to two hatchery facilities (Jonkershoek Fish Hatchery and Pirie Hatchery), with small numbers (20–40) of fish subsequently used to establish individual populations (Harrison 1936). Similar patterns of low genetic variation were noted for bluegill (*L. macrochirus*) in Japan and Korea, where all 72 reported populations directly descended from 15 individuals imported from Iowa, USA (Kawamura et al. 2006). Low propagule pressure is thus a likely explanation for the lower observed genetic diversity than in their native ranges (Roman and Darling 2007).

Additional factors that could further reduce genetic diversity include post-introduction dispersal mechanisms, with many populations that established subsequently resulting from unsanctioned or angler-mediated translocations (e.g., Hargrove et al. 2015). For example, Kawamura et al. (2010) observed a pattern of isolation-by-distance (i.e., genetic differentiation among populations increasing linearly with geographic distance) among Japanese bluegill (*L. macrochirus*) populations, whereby genetic bottlenecks increased with geographical distance from founding stocks (Lake Biwa) and time since establishment. Smallmouth bass (*M. dolomieu*) in eastern Japan displayed relatively high levels of diversity, whereas locations in western Japan were largely fixed for individual haplotypes (Sato et al. 2007). Patterns of genetic diversity among bluegill (*L. macrochirus*) in Korea did not follow expectations based on biogeographic barriers and suggested that post-introduction spread (i.e., secondary introductions) by local people for aquaculture and fishing was likely responsible for the observed patterns (Lau et al. 2009). However, genetic bottlenecks and low genetic diversity have not impeded centrarchid establishment or spread due to large-effect loci and cryptic genetic variation (Dlugosch et al. 2015; Estoup et al. 2016).

Genetic admixture is another common feature of many non-native centrarchid populations, arising from multiple introduction events. For example, genetic variability and divergence among largemouth bass (*M. nigricans*) in Japan evidenced strong differentiation between two prefectures, supporting the hypothesis that distinct genetic clusters were the consequence of multiple introductions (Takagi et al. 2007). Multiple distinct genetic clusters among populations of both smallmouth (*M. dolomieu*) and largemouth bass (*M. nigricans*) introduced in South Africa suggested several introduction events (Hargrove et al. 2017; Diedericks et al. 2018b). However, the distinct genetic clusters of the South African largemouth bass (*M. nigricans*) resulted from interspecific hybridisation with Florida bass (*M. salmoides*), rather than admixture between multiple introductions (Hargrove, Weyl, et al. 2019).

Given the high incidence of interspecific hybridisation among Centrarchidae species, it can be difficult to discriminate between morphologically similar species (e.g., largemouth bass *M. nigricans* and Florida bass *M. salmoides*) and their hybrids. Thus, where centrarchids co-occur, genetic tools are important for identifying the species present and estimating hybridisation rates. For example, largemouth bass (*M. nigricans*) was initially introduced to South Africa in the 1920s, and by the 1970s was

present in nearly every province in the country, whereas Florida bass (*M. salmoides*) was imported much later (1980s) to enhance existing largemouth bass (*M. nigricans*) fisheries (Ellender et al. 2014). However, the distribution and co-occurrence of these species was unknown due to poor stocking records (Weyl et al. 2017), with mitochondrial DNA (mtDNA) revealing Florida bass (*M. salmoides*) to be widespread and frequently co-occurred with largemouth bass (*M. nigricans*) in the same water body (45% of locations) (Weyl et al. 2017). Introgression of Florida bass (*M. salmoides*) alleles into existing populations of largemouth bass (*M. nigricans*) has also been observed in these waters and across a broad geographic range, from the Cape Floristic region of South Africa to Mozambique (Hargrove, Weyl, et al. 2019). Additionally, several populations previously considered pure largemouth bass (*M. nigricans*) based on mtDNA sequences (e.g., Weyl et al. 2017) were found to consist of exclusively fertile hybrids according to SNP data, and hybridised populations were generally dominated by a single hybrid class (e.g., late-stage backcrosses; Hargrove, Weyl, et al. 2019).

3.5 | Impacts

3.5.1 | Impact Types and Mechanisms

Of the 30 non-native Centrarchidae species, 20 have recorded impacts according to GFID (Haubrock et al. 2025b). Reported impacts are primarily ecological ($n=20$ species), followed by socio-cultural (5), and economic (5). Among these species, 13 have been reported as having exclusively ecological impacts, while two species have impacts spanning both economic and ecological domains [i.e., rock bass (*A. rupestris*); bluegill (*L. macrochirus*)] and two species have impacts spanning both social and ecological domains [i.e., redbreast sunfish (*L. auriatus*); smallmouth bass (*M. dolomieu*)] (Figure 7a). Finally, three species have been reported to have impacts across all categories [i.e., green sunfish (*L. cyanellus*); orangespotted sunfish (*L. humilis*); largemouth bass (*M. nigricans*)]. For mechanisms of impacts, 'Predation' (20) is the most reported, followed by 'Competition' (12), 'Hybridisation' (10), 'Transmission of disease' (6) and 'Habitat alteration' (5). The other reported mechanisms are related to no more than five species. Several species are reported to have impacts through multiple mechanisms, with green sunfish (*L. cyanellus*) associated with all mechanisms (Figure 7b).

Ecological impacts of non-native Centrarchidae species are wide-ranging and can arise from both direct and indirect interactions that affect native biodiversity, habitat quality and ecosystem functions. Species such as smallmouth bass (*M. dolomieu*) and largemouth bass (*M. nigricans*) have been implicated in declines in native fish species diversity in areas where they are introduced (Woodford et al. 2005; Pereira and Vitule 2019). The most frequently reported mechanism of impacts for all Centrarchidae found outside of their native ranges is predation on aquatic and semi-aquatic fauna (e.g., fish, amphibians) including fish eggs (Figure 7b; García-Berthou and Moreno-Amich 2000; Bosman 2003; Preau et al. 2017). Studies on smallmouth bass (*M. dolomieu*) in the Pacific Northwest have emphasized their predation on salmon smolts migrating through the Columbia River hydropower corridor. Reported predation levels vary

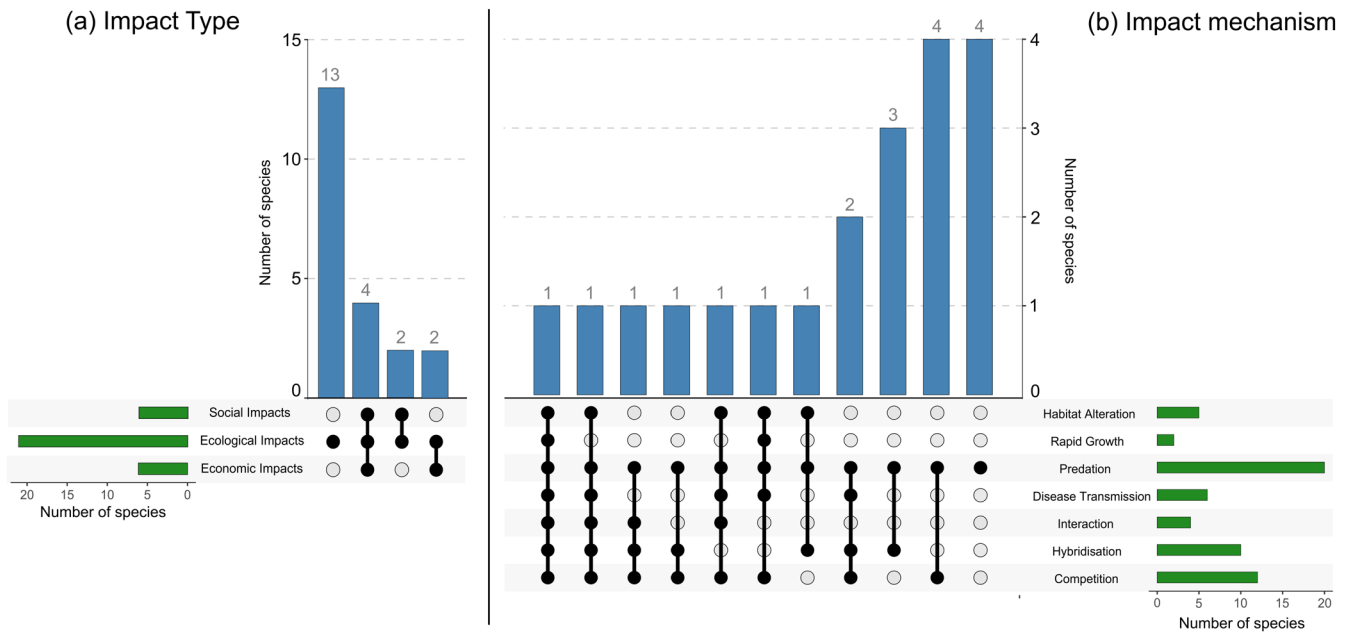


FIGURE 7 | Upset plot showing Centrarchidae species impact (a) and impact mechanism (b) based on information reported in the *Global Fish Invasion Database* (GFID; Haubrock et al. 2025b). Horizontal bars show the total number of species for each impact type and mechanism. Vertical bars show the number of species with a single (black dot) or multiple (connected black dots) impact type or mechanism.

widely, from 0% to 35% of the total wild salmon run (Sanderson et al. 2009). This variation is largely influenced by abiotic conditions such as temperature, water clarity, and flow during periods of species overlap (Carey et al. 2011), as well as by the size and origin of smolts available to bass (Fritts and Pearsons 2006). The most significant predation impacts have been observed on small subyearling ocean-type Chinook salmon (*Oncorhynchus tshawytscha*), which migrate during warmer conditions that permit bass activity ($> 10^{\circ}\text{C}$; Fritts and Pearsons 2004). In contrast, predation is much lower—or absent—on larger yearling salmon smolts that migrate earlier in the season, when river temperatures remain cooler. In regions where no comparable predators occur, the severity of predatory impacts may be driven by the evolutionary naïveté of the prey species, including behavioural adaptations to avoid native predators that increase their vulnerability to invasive bass predation (Ellender et al. 2018).

Another mechanism that directly affects native species is competition, although the strength of this interaction is highly variable depending on the species involved and the environmental context. For example, based on an analysis of stable isotopes and fatty acids, Rubenson et al. (2020) reported minimal trophic overlap between juvenile Chinook salmon (*O. tshawytscha*) and smallmouth bass (*M. dolomieu*) in a tributary of the Columbia River. Non-native species can also bring novel parasites and diseases that can infect native species further reducing native species fitness (e.g., Rubtsova 2015; Goswami et al. 2021). This additional stress—alongside increased predation pressure—can lead to food web simplification that decreases habitat resilience to disturbances (Kim et al. 2021). Non-native fish species have been implicated in the alteration of physicochemical properties and community structure of invaded environments (da Silva et al. 2024), with non-native centrarchids able to enhance resuspension of sediments and

nutrients through benthic feeding, increasing water turbidity and negatively impacting submerged vegetation (Adámek and Maršálek 2013; Godinho and Ferreira 2014). Unmanaged population growth of non-native fishes like centrarchids in invaded ecosystems can intensify these effects and alter nutrient cycling (da Silva et al. 2024).

As most studies on non-native species tend to focus on ecological consequences, socio-economic dimensions remain understudied. For centrarchids, only a few species have been explicitly reported to have economic impacts: largemouth bass (*M. nigricans*), pumpkinseed (*L. gibbosus*), and bluegill (*L. macrochirus*) are estimated to have incurred costs of at least US\$ 5.4 million since 1960, largely due to post-introduction management efforts (Haubrock et al. 2022). For cultural impacts, displacement of native species embedded in traditions of different societies may lead to cultural disruptions, loss of cultural identity, or the erosion of traditional knowledge (Jarić et al. 2025). This may affect traditional cuisine and how indigenous people interact with nature (Pfeiffer and Voeks 2008). For example, there is a preconceived notion that some non-native fish species are distasteful (Seaman et al. 2022). Although non-native fish can be accepted by local communities, non-native species are generally less preferred than natives (Cerveira et al. 2022). Also, changes in species composition because of non-native species introduction can affect the perceived quality of fishing areas, as recreational fishers tend to select sites based on the availability of preferred species (Schramm Jr et al. 2003). The introduction of non-native species can lead to shifts in species composition, reducing the availability of these preferred targets, thereby reducing the overall fishing experience and satisfaction (Ready et al. 2018). However, it should also be noted that the general public may not necessarily identify particular species or their nativeness correctly (Lipták et al. 2024).

3.5.2 | Assessments and Screenings

According to the country-specific checklist provided by GRIIS, 13 non-native Centrarchidae species are identified as invasive (i.e., a species showing credible evidence of environmental impacts and/or recognized as widespread, rapidly spreading or in high abundance—on the basis that high abundance or rapid population growth is strongly associated with ecological impacts; *sensu* Pagad et al. 2022) in at least one country where they were introduced. Largemouth bass (*M. nigricans*) is considered invasive in 21 countries, followed by pumpkinseed (*L. gibbosus*) ($n = 19$ countries), smallmouth bass (*M. dolomieu*) ($n = 6$), and bluegill (*L. macrochirus*) ($n = 5$). Green sunfish (*L. cyanellus*) and black crappie (*P. nigromaculatus*) are reported as invasive in two countries, while rock bass (*A. rupestris*), redbreast sunfish (*L. auritus*), warmouth (*L. gulosus*), dollar sunfish (*L. marginatus*), redear sunfish (*L. microlophus*), spotted sunfish (*L. punctatus*) and white crappie (*P. annularis*) are recorded as invasive in one country each (Table S5). However, although 17 of the 30 non-native Centrarchidae species are present in countries outside their native ranges, only 10 have been screened for their risk using tools such as AS-ISK (Vilizzi et al. 2021) and DOSI (Soto et al. 2024).

Among centrarchids, pumpkinseed (*L. gibbosus*) was the sole species that was both assessed and deemed sufficiently significant to warrant inclusion in the EU Regulation 1143/2014 list of Union concern species (European Commission 2019). Available evidence from the application of AS-ISK (Vilizzi et al. 2021) indicates that Centrarchidae species generally exceed thresholds for both Basic Risk Assessment and Basic Risk Assessment with Climate Change Assessment, set at 14.7 and 17.7, respectively (Vilizzi et al. 2021) (Table S3). For example, rock bass (*A. rupestris*) scored 8.5 in England (medium risk; Vilizzi et al. 2021) but 19 in Türkiye (high risk; Tarkan, Vilizzi, et al. 2017), reflecting strong context dependency. Pumpkinseed (*L. gibbosus*), the most frequently screened centrarchid, consistently shows very high scores: from 17.7 to nearly 50 in Lakes Ohrid and Prespa (Bakiu et al. 2022; Trajanovski et al. 2023) and 40–53 in most European regions (Glamuzina et al. 2017; Tarkan, Sari, et al. 2017; Tarkan, Vilizzi, et al. 2017; Radočaj et al. 2021; Vilizzi et al. 2021). These values exceed the global freshwater fish average by more than twofold, in agreement with its well-documented invasive potential. Other species of the genus *Lepomis* also show high risks:

bluegill (*L. macrochirus*) and green sunfish (*L. cyanellus*) scored between 30 and 35.5 in Japan and China (Vilizzi et al. 2021; Yu et al. 2024). Smallmouth bass (*M. dolomieu*) scored very low in Finland and Japan (≤ 5.5 ; Vilizzi et al. 2021) but much higher in Türkiye (21; Tarkan, Vilizzi, et al. 2017) and England (37; Vilizzi et al. 2021). By contrast, largemouth bass (*M. nigricans*) consistently exceeds thresholds (> 40 across Europe and Türkiye; Glamuzina et al. 2017; Tarkan, Vilizzi, et al. 2017; Radočaj et al. 2021; Vilizzi et al. 2021), whereas white crappie (*P. annularis*) and black crappie (*P. nigromaculatus*) were only assessed in Türkiye with mixed results (33 vs. 17, respectively; Tarkan, Vilizzi, et al. 2017). The Dispersal-Origin-Status-Impact (DOSI) framework (Soto et al. 2024), which evaluates the dispersal, establishment and realized impacts of non-native populations, was only applied to pumpkinseed (*L. gibbosus*) in Türkiye. Populations were ranked as medium priority in Lake Gala and Sığircı Reservoir (Tarkan et al. 2024), moderate in Lake Manyas and Lake Ulubat, and medium-high in the Kocaçay Delta (Saç et al. 2025), reflecting localized variation but overall limited ecological impacts. In South Africa, a retrospective risk analysis using the Fish Invasiveness Screening Kit (FISK; Copp et al. 2005) assigned the five established Centrarchidae species scores between 15 (Medium) and 25 (High) in invasion risk (Marr et al. 2017).

3.5.3 | Current and Future Risks

The distribution of suitable habitats provides a first indication of regions most at risk from non-native centrarchid introductions. Our SDM based on available GBIF occurrence records of centrarchids showed that habitat suitability was highest in North America, particularly in the eastern United States of America, coinciding with the family's native range (Figure 8). Additional areas of elevated suitability were identified in parts of South America, Europe, and eastern Asia. In contrast, much of Africa, northern Eurasia, and Australia exhibited generally low suitability values. However, it should be noted that SDMs of invasive species are particularly uncertain (Elith 2017; Srivastava et al. 2019) and our results might underestimate habitat suitability for many species that have not been widely introduced and for many regions with few introductions. These areas of predicted suitability overlap with pathways driven by the economic importance of centrarchids, particularly their role in aquaculture

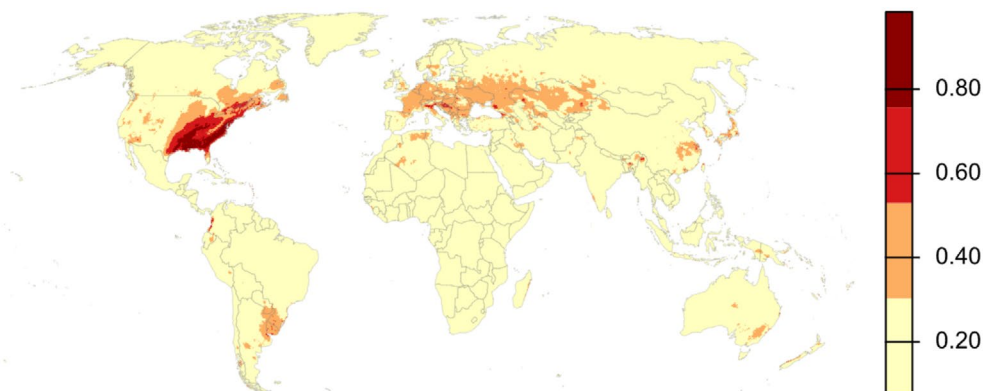


FIGURE 8 | Global habitat suitability of non-native Centrarchidae derived from a species distribution model (SDM) based on available GBIF occurrence records. Warmer colours indicate areas of higher predicted suitability. See Section 2.5 for methodological details of the SDM.

and the ornamental trade. Indeed, the economic importance of centrarchids directly influences their likelihood of being introduced outside their native environments (Lima et al. 2018). For example, the role of largemouth bass (*M. nigricans*) as a viable source of protein and income for people in several countries has led to the development of aquaculture facilities and hatchery production outside its native range (Hussein et al. 2020; Pěnka et al. 2021), creating a sustained propagule pressure that increases the possibility of establishment (Simberloff 2009).

Currently, largemouth bass (*M. nigricans*) is an important aquaculture fish species in China, with production reaching ~888,000 t in 2020 (FAO 2025) and an annual production increase of 9.8% (Fang et al. 2023). Other centrarchids used in aquaculture include redbreast sunfish (*L. auritus*), green sunfish (*L. cyanellus*), warmouth (*L. gulosus*), bluegill (*L. macrochirus*) and smallmouth bass (*M. dolomieu*) (Welcomme 1988). Also, the presence of centrarchids, such as pumpkinseed (*L. gibbosus*), in the ornamental and aquarium fish trade can considerably increase the potential of these species to be introduced to more countries outside their native ranges (Maceda-Veiga et al. 2016; Dickey et al. 2023). Currently, pumpkinseed (*L. gibbosus*) is present in at least 40 countries. However, while its keeping, importing, selling, breeding, and growing have been restricted in the European Union (EU) under Regulation 1143/2014, data suggest that at least 107 countries are involved in the global aquarium trade, worth US\$ 395.97 million in 2021 (Jain and Karunasagar 2025). Even if the EU Regulation were to successfully prevent new introductions of pumpkinseed (*L. gibbosus*) in Europe, it is likely that the aquarium trade would shift to another colourful Centrarchidae species, as has been observed for pond sliders (Rato et al. 2025).

Recreational angling remains one of the strongest drivers of intentional introductions of centrarchids, as these species are highly valued as sportfish in many regions (Ellender et al. 2014; Carpio et al. 2019). Stocking programmes, both legal (Robbins and MacCrimmon 1974; Welcomme 1988) and illegal (Rahel and Smith 2018; Banha et al. 2024), have also historically moved individuals far beyond their native ranges, often with little consideration of ecological consequences. The availability of human pathways, paired with projected warming of freshwater systems and hydrological shifts (such as reduced flow or extended warm seasons; Kirk et al. 2022), are likely to make previously unsuitable habitats thermally accessible for centrarchid establishment (Rabitsch et al. 2013; Bae et al. 2018). This may facilitate poleward or altitudinal range expansion (Winkowski et al. 2024), creating new invasion fronts where native fish and communities are unadapted to the ecological impacts of centrarchids (Tarkan et al. 2021; Emiroğlu et al. 2023). For example, both laboratory and field experiments have shown that juvenile Chinook salmon (*O. tshawytscha*) are less able to recognize the chemical cues of invasive smallmouth bass (*M. dolomieu*) compared with native northern pikeminnow (*Ptychocheilus oregonensis*; Kuehne and Olden 2012). Where multiple non-native centrarchids co-occur, hybridisation among non-natives and with closely related native species may lead to genetic introgression and the potential loss of unique local genotypes (Bangs et al. 2018). Although hybridisation may also produce more competitive

hybrids, further altering community dynamics and complicating management, these risks are often underreported due to limited monitoring of genetic impacts in invaded ecosystems (Cucherousset and Olden 2011).

3.5.4 | Interactions

3.5.4.1 | Interactions With Other Non-Native Species. The occurrence, abundance, spread and impacts of non-native centrarchids can be affected by interactions with other non-native species, which can be synergistic, additive, or antagonistic (Rauschert and Shea 2012), with the presence of some non-native species facilitating invasions of others (i.e., invasion meltdown; Simberloff and Von Holle 1999). For example, non-native pumpkinseed (*L. gibbosus*) can facilitate American bullfrog (*Lithobates catesbeianus*) tadpole survival by reducing predatory macroinvertebrate densities (Adams et al. 2003), although predation by Florida bass (*M. salmoides*) and green sunfish (*L. cyanellus*) on bullfrog tadpoles has been reported (Kruse and Francis 1977; Evenson and Kruse 1982). Similarly, bluegill (*L. macrochirus*) has often been co-introduced with largemouth bass (*M. nigricans*) in Japan to ensure a steady food source for the permanent establishment of largemouth bass (*M. nigricans*) to ultimately support sportfishing. The trophic polymorphism of bluegill (*L. macrochirus*) enables it to prey upon both benthic animals and zooplankton, with potential trophic impacts of the carnivorous largemouth bass (*M. nigricans*) cascading through the ecosystem (Noda and Maruyama 2014).

Antagonistic interactions can inhibit the establishment, spread, and impact of another non-native species (i.e., invasional interference; Yang et al. 2011). Non-native largemouth bass (*M. nigricans*) in Japanese farm ponds exert strong top-down predatory pressures that can limit the abundances of the non-native red swamp crayfish (*Procambarus clarkii*), and consequently mitigate its negative impacts on macrophyte cover (Maezono et al. 2005). Additionally, largemouth bass (*M. nigricans*) foraging efficacy decreases with increasing cover of the invasive hydrophyte *Egeria densa* (Ferrari et al. 2014). Antagonistic interactions can also occur among fish species, as indicated by the large isotopic niche overlap measured between largemouth bass (*M. nigricans*) and non-native smallmouth bass (*M. dolomieu*), the non-native pike chain pickerel (*Esox niger*), and the native yellow perch (*Perca flavescens*) in the Wolastoq River, New Brunswick, Canada (Culbertson et al. 2025). Nelson et al. (2017) further experimentally showed that the growth of bluegill (*L. macrochirus*) declined in the presence of bighead carp (*Hypophthalmichthys nobilis*), an obligate planktivore, owing to the latter's dominance of planktonic food sources. Conversely, bighead carp (*H. nobilis*) growth increased when bluegill (*L. macrochirus*) occurred at low densities. However, Collins et al. (2017) found the opposite, highlighting the importance of context dependence in invasion impacts (Catford et al. 2022; Haubrock et al. 2024). Synergistic and antagonistic interactions can also occur simultaneously when multiple non-native species co-exist. In the Willamette Valley (Oregon, United States of America), non-native centrarchids and bullfrogs were found to cumulatively impact native northern red-legged frogs (*Rana aurora*). These effects were however mediated by invasive reed

canarygrass (*Phalaris arundinacea*), as similar to *E. densa*, reed canarygrass (*P. arundinacea*) is assumed to lower predatory efficacy (Rowe et al. 2019). It can be expected that in most cases, however, the effects of multiple co-occurring non-native Centrarchidae species are additive, where their effects are independent of each other. For instance, dietary niche overlap between pumpkinseed (*L. gibbosus*) and largemouth bass (*M. nigricans*) in Lake Arreo (Spain) was found to be low (Haubrock et al. 2019), suggesting the predatory and competitive impacts of both species are relatively independent of each other.

Hybridisation can occur not only between non-native and native species (Meraner et al. 2013; Galvez-Bravo et al. 2023), but also among non-native species (Diedericks et al. 2018a; Brys et al. 2025), and has been observed across multiple taxonomic groups of fish, including centrarchids (Section 3.2.3). Hybridisation events can contribute to population extirpation due to continuous introgression and a lack of reproductive isolation (Bolnick 2009). For instance, Bangs et al. (2018) found that introductions of Alabama bass (*M. henshalli*) caused extensive introgression to the native Batram's bass (*Micropterus* sp. cf. *coosae*) populations, resulting in local extirpations. Among Centrarchidae species, over 30 natural hybrid combinations have been described within the family, most of them occurring among species of the same genus (Bolnick 2009). In many cases (Table 4), these hybrids are not introduced per se but result from introducing one or more Centrarchidae species into a novel range where they come into contact with native or previously isolated congeners. This process can lead to extensive introgression and even genetic swamping of rare endemics, representing an insidious yet concerning consequence of species introductions (Theodoropoulos et al. 2025). For example, Guadalupe bass (*M. treculii*) populations in Texas have been reported to consist of 20%–46% hybrids following the introduction of largemouth bass (*M. nigricans*) and smallmouth bass (*M. dolomieu*), threatening the genetic integrity of the native species (Morizot

et al. 1991). Similarly, hybridisation with introduced spotted bass (*M. punctulatus*) has contributed to the local extirpation of native smallmouth bass (*M. dolomieu*) in Georgia reservoirs (Avisé et al. 1997), illustrating that hybridisation is a mechanism of impact that can irreversibly alter native gene pools, complicate management, and exacerbate biodiversity loss (Rhymer and Simberloff 1996; Allendorf et al. 2001; Theodoropoulos et al. 2025). However, hybridisation between largemouth bass (*M. nigricans*) and Florida bass (*M. salmoides*) is likely under-detected outside currently considered regions (Table 4), because stocking histories are often incomplete and morphological identification is unreliable without genetic confirmation. Where such hybrids occur, trait combinations plausibly increase invasion potential (e.g., greater cold tolerance inherited from *M. nigricans* together with rapid growth and fishery-selected performance associated with *M. salmoides*), potentially amplifying predation pressure, competitive displacement, and management difficulty across invaded food webs (Khosa et al. 2020; Lutz-Carrillo et al. 2023).

3.5.4.2 | Interactions With External Disturbances. Disturbances are events that disrupt ecosystem structure and function, shaping evolution and community dynamics (Pickett et al. 1989; Battisti et al. 2016), and influencing the occurrence and course of successful non-native fish introductions (Meador et al. 2003). They can be natural or human-induced, but anthropogenic disturbances often exceed natural variability and can drive ecosystems into alternative states (Pickett and White 1985; Gunderson 2000). For example, dam construction alters hydrology, reduces resilience and opens new niches that facilitate invasions (Lozon and MacIsaac 1997; Dunham et al. 2003; Liew et al. 2016; Meyer et al. 2021). Disturbances such as flow regulation, impoundments, pollution and climate change promote centrarchid invasions (Almeida et al. 2009; Stewart et al. 2016; Pereira and Vitule 2019; Kang et al. 2023; Long and Seguy 2024; Taylor et al. 2025).

TABLE 4 | Main examples of centrarchid hybrids resulting from introduction of at least one species outside its native range.

Hybrid	Country	References
<i>Lepomis macrochirus</i> × <i>microlophus</i>	United States of America	Cross and Moore (1952)
<i>Micropterus cataractae</i> × <i>henshalli</i>	United States of America	Taylor et al. (2025)
<i>Micropterus coosae</i> × <i>dolomieu</i>	United States of America	Pipas and Bulow (1998)
<i>Micropterus dolomieu</i> × <i>henshalli</i>	United States of America	Sammons et al. (2023)
<i>M. dolomieu</i> × <i>punctulatus</i>	United States of America	Pierce and Van Den Avyle (1997)
<i>M. dolomieu</i> × <i>salmoides</i>	South Africa, United States of America	Morizot et al. (1991); Diedericks et al. (2018a)
<i>M. dolomieu</i> × <i>treculii</i>	United States of America	Morizot et al. (1991); Bean et al. (2013)
<i>M. dolomieu</i> × <i>velox</i>	United States of America	Taylor et al. (2025)
<i>M. nigricans</i> × <i>salmoides</i>	Botswana, Japan, Mozambique, South Africa, United States of America	Yokogawa et al. (2005); Hargrove, Weyl, et al. (2019); Hargrove, Rogers, et al. (2019); Khosa et al. (2022)
<i>M. sp. cf. coosae</i> × <i>dolomieu</i>	United States of America	Bangs et al. (2018)
<i>M. sp. cf. coosae</i> × <i>henshalli</i>	United States of America	Bangs et al. (2018); Peoples et al. (2021)
<i>M. treculii</i> × <i>salmoides</i>	United States of America	Morizot et al. (1991)

Hydrological alterations, especially dam construction, create lentic habitats and fragment river networks, favouring lentic-adapted centrarchids such as largemouth bass (*M. nigricans*) (Aday et al. 2009; Liew et al. 2016; Bae et al. 2018; Kang et al. 2023). In Mediterranean and arid-climate rivers and parts of China and Japan, reservoirs have consistently enabled successful establishment and spread of largemouth bass (*M. nigricans*) and pumpkinseed (*L. gibbosus*) (Han et al. 2008; Ribeiro and Collares-Pereira 2010; Clavero et al. 2013; Kang et al. 2023). In Japan, both *M. nigricans*, *M. salmoides* and hybrids are present (Yokogawa 1998; Yokogawa et al. 2005). Within the watersheds of Lake Lanier (Georgia) and Lake Tenkiller (Oklahoma, United States of America), impoundments have been shown to facilitate upstream tributary invasions by *Micropterus* species and hybridisation with native congeneric fluvial taxa (Taylor et al. 2025). Similarly, non-native centrarchids are frequently associated with degraded watersheds in the New Jersey Pinelands, United States of America, particularly those characterized by elevated pH and altered upstream land use (Bunnell and Zampella 2008). Pollution can also shift community composition: in Wyoming, non-native green sunfish (*L. cyanellus*) abundance increased near oil and gas development zones, likely due to tolerance to degraded conditions (Stewart et al. 2016).

Climate change compounds these effects by warming waters and driving demand for additional reservoirs, further facilitating centrarchid invasions (Johnson et al. 2008; Ilheu et al. 2014; Long and Seguy 2024), their poleward migration (Rolls et al. 2017), and their ecological impacts (Van Zuiden and Sharma 2016; Kirk et al. 2022). For example, Rubenson and Olden (2020) combined a species distribution model with environmental DNA to show that the critical spawning and rearing habitat of most Pacific salmonids, especially Chinook salmon (*O. tshawytscha*) and sockeye salmon (*Oncorhynchus nerka*), overlap with established year-round smallmouth bass (*M. dolomieu*) populations in the Columbia River Basin, and that under a moderate climate change scenario, smallmouth bass (*M. dolomieu*) distribution is predicted to expand extensively by 2080. Similarly, temperature-driven range expansions are forecast for north temperate lakes in Canada (Sharma et al. 2007), which may promote novel species competitive interactions (Van Zuiden et al. 2016).

Droughts and floods are also reported to alter the balance between native fish and non-native centrarchids (Bernardo et al. 2003). Accidental releases from failed aquaculture attempts have seeded new populations in Chinese rivers (Kang et al. 2023). More subtly, anthropogenic noise such as that produced by boats has been found to decrease the feeding rates of pumpkinseed (*L. gibbosus*), although habituation can eliminate this effect (Rojas et al. 2021). Collectively, these disturbances may lower biotic resistance, accelerate establishment, and magnify ecological impacts—illustrated in the Iberian Peninsula, where dam construction is often followed by rapid introductions and establishment of largemouth bass (*M. nigricans*) and pumpkinseed (*L. gibbosus*) (Almeida et al. 2009; Ribeiro and Collares-Pereira 2010; Marr et al. 2013).

Disturbances often increase the spread and impact of centrarchids by reducing habitat complexity and native biodiversity, which gives invasive species fewer competitors and predators,

enabling centrarchids to dominate prey resources and alter food webs (Copp et al. 2017; Costantini et al. 2023). Barrier removal (e.g., dams) can enable centrarchids to colonize previously inaccessible upstream reaches, accelerating range expansion and shifting community structure towards lentic-tolerant species (Terêncio et al. 2021; Dolan et al. 2025). In systems already stressed by pollution or altered flow regimes, centrarchids tend to have higher survival and growth rates, intensifying predation pressure and suppression of native species (Copp et al. 2017). Indeed, reduced productivity and biodiversity at lower trophic levels in lake food webs may facilitate the establishment and success of opportunistic non-native Centrarchidae species (Costantini et al. 2018).

3.5.5 | Disease-Causing Agents

Non-native Centrarchidae species host both native and non-native parasites in areas they invade. This can be either through co-introduction of parasitic organisms (i.e., parasitic spillover) (Lymbery et al. 2014) or by amplifying the transmission dynamics of native (and non-native) parasites in invaded areas (i.e., parasite spillback; Kvach et al. 2021). Parasitic species can switch hosts in introduced habitats (Ondračková 2016). The lack of natural defence mechanisms of native fishes against co-introduced parasites makes them more vulnerable to these organisms (Gozlan et al. 2005). In the case of centrarchids, several co-introduced parasites have been reported (Table 5). For example, the first record of *Onchocleidus dispar* in the Dnieper river, Ukraine, was reportedly co-introduced with pumpkinseed (*L. gibbosus*) (Rubtsova 2015). Japan also reported co-introduction of *O. dispar*, *O. ferox* and *Actinocleidus fergusonii* with pumpkinseed (*L. gibbosus*) and bluegill (*L. macrochirus*) (Maneepitaksanti and Nagasawa 2012). The most widespread Centrarchidae species, largemouth bass (*M. nigricans*), is also implicated in the co-introduction of *O. principalis* in Portugal (Ondračková et al. 2020). Although empirical evidence of parasites co-introduced with centrarchids spilling over to native species is scarce (Esposito et al. 2023), the transfer of parasites from co-existing Centrarchidae species in non-native ranges has been observed (Ondračková et al. 2020). For example, bluegill (*L. macrochirus*), pumpkinseed (*L. gibbosus*), smallmouth bass (*M. dolomieu*) and largemouth bass (*M. nigricans*) are utilised by *Neogergasilus japonicus* as alternative hosts in the native and non-native ranges of the parasite (Nagasawa and Obe 2015; Nagasawa and Sato 2015). Other parasites, like the cestode *Bothriocephalus claviceps*, an eel (*Anguilla* spp.) parasite have been found to use pumpkinseed (*L. gibbosus*) (Scholz 1997) as a definitive host (Kvach et al. 2021). However, several studies show that non-native centrarchids have limited native parasite acquisition (Ondračková, Kvach, et al. 2019).

3.6 | Human Benefits

Centrarchids are now the most popular recreational fishes in Central and North America, shaping regional fisheries culture and management (Tingley III et al. 2019). In the US, 9.6 million anglers and 117 million fishing days generate ~\$41.9 billion in revenue annually and sustain over 525,000 jobs, with licence revenues

TABLE 5 | List of parasitic organisms co-introduced with Centrarchidae in non-native areas.

Parasite	Centrarchidae host	Study location	References
<i>Onchocleidus dispar</i>	<i>L. gibbosus</i> ; <i>L. macrochirus</i> ; <i>M. nigricans</i>	Austria; Bulgaria; Croatia; Czech Republic; Italy; Ukraine; UK; Japan; Portugal; Slovakia; South Africa; Türkiye; France; Germany	Galli et al. (2007); Hockley et al. (2011); Ondračková et al. (2011); Maneepitaksanti and Nagasawa (2012); Havlátová et al. (2015); Rubtsova (2015); Truter et al. (2017); Ondračková, Fojtů, et al. (2019); Ondračková et al. (2020); Ondračková et al. (2021); Kvach et al. (2024)
<i>Onchocleidus acer</i>	<i>L. gibbosus</i>	France	Havlátová et al. (2015)
<i>Clavunculus bursatus</i>	<i>M. nigricans</i>	South Africa	Truter et al. (2017)
<i>Cleidodiscus robustus</i>	<i>L. gibbosus</i>	France	Havlátová et al. (2015)
<i>Onchocleidus principalis</i>	<i>L. gibbosus</i> ; <i>M. nigricans</i>	Italy; Portugal; South Africa; UK	Maitland and Price (1969); Galli et al. (2007); Truter et al. (2017); Ondračková et al. (2020)
<i>Onchocleidus similis</i>	<i>L. gibbosus</i>	Austria; Bulgaria; Croatia; Czech Republic; France; Germany; Italy; Norway; Slovakia; Ukraine	Sterud and Jørgensen (2006); Galli et al. (2007); Ondračková et al. (2011); Havlátová et al. (2015); Kvach et al. (2018a); Ondračková, Fojtů, et al. (2019); Ondračková et al. (2021)
<i>Onchocleidus ferox</i>	<i>L. gibbosus</i>	Japan	Maneepitaksanti and Nagasawa (2012)
<i>Onchocleidus furcatus</i>	<i>M. nigricans</i>	South Africa	Truter et al. (2017)
<i>Actinocleidus fergusonii</i>	<i>L. gibbosus</i>	Japan	Maneepitaksanti and Nagasawa (2012)
<i>Actinocleidus oculatus</i>	<i>L. gibbosus</i>	France; Germany; Italy	Galli et al. (2007); Havlátová et al. (2015); Ondračková, Kvach, et al. (2019)
<i>Actinocleidus recurvatus</i>	<i>L. gibbosus</i>	Austria; Croatia; France; Germany; Italy; Slovakia	Galli et al. (2007); Ondračková et al. (2011); Havlátová et al. (2015); Ondračková, Kvach, et al. (2019); Ondračková et al. (2021)
<i>Myxobolus dechtiari</i>	<i>L. gibbosus</i>	Türkiye	Kvach et al. (2024)
<i>Neogerasilus japonicus</i>	<i>L. gibbosus</i> ; <i>L. macrochirus</i> ; <i>M. nigricans</i>	Czech Republic; Japan	Nagasawa and Sato (2015); Ondračková, Fojtů, et al. (2019)
<i>Gyrodactylus avalonia</i>	<i>L. gibbosus</i>	Ukraine	Kvach et al. (2018a)
<i>Gyrodactylus macrochiri</i>	<i>L. gibbosus</i>	France	Havlátová et al. (2015)
<i>Posthodiplostomum centrarchi</i>	<i>L. gibbosus</i> ; <i>M. nigricans</i>	Germany; Türkiye; Ukraine	Kvach et al. (2018b); Ondračková, Kvach, et al. (2019); Kvach et al. (2024)
<i>Synleithrium fusiformis</i>	<i>M. nigricans</i>	South Africa	Truter et al. (2017)

funding much of the state-level fish and wildlife conservation (Carey et al. 2011; Seguy and Long 2021; Long and Seguy 2024). Stocked populations fuel tournaments and trophy fisheries, contributing notable economic gains at the state level (Oregon 2006: ~US\$23.3 M; Washington 2006: ~US\$32.6 M) and single lakes such as Lake Fork, Texas, producing US\$27.5 million in annual income and sustaining 163 jobs (Costantini et al. 2023). Moreover, hybridization programs [e.g., stocking Florida bass (*M. salmoides*) into largemouth bass (*M. nigricans*) ranges] are used to create faster-growing trophy fish that attract angling expenditures (Carey et al. 2011; Seguy and Long 2021).

As a result of their fame as sought-after angling trophies, many species have been intentionally introduced to support fisheries, either for food or recreation (Kvach et al. 2018b; Carpio et al. 2019; Haubrock et al. 2025a). Although these introductions often exert pressure on native biodiversity and impose economic costs (Haubrock et al. 2022), they also provide societal benefits, mainly through tourism, gear sales, and tournaments, especially where sufficiently attractive native sportfish are lacking (Driscoll and Myers 2014; Costantini et al. 2023; Long and Seguy 2024). In Portugal, largemouth bass ranks among the most common freshwater species for consumption,

favoured for its fast growth, desirable flesh quality, and strong market demand (Jorge et al. 2022). Especially, largemouth bass (*M. nigricans*) has been widely introduced worldwide for recreational fishing (Hickley et al. 2015; Costantini et al. 2023) and for its high economic and cultural value (Chen et al. 2003; Hannonen and Hoogendoorn 2022; Melstrom et al. 2023). Additionally, largemouth bass (*M. nigricans*) is one of the most preferred species among anglers across the Iberian Peninsula (Banha et al. 2017, 2024). In China, it has also become a key aquaculture species with over 700,000t produced annually (Costantini et al. 2023) and substantial ongoing research (Bai and Li 2018; Wang et al. 2024; Li et al. 2025). Globally, centrarchids are estimated to have a total economic value of approximately US\$ 2 billion (U.S. Geological Survey 2025). Other Centrarchidae species, such as pumpkinseed (*L. gibbosus*) and the blackbanded sunfish (*Enneacanthus chaetodon*), are prized aquarium and garden pond fish (Maceda-Veiga et al. 2013).

Despite ecological risks, managers and anglers often regard them as economically valuable (Seguy and Long 2021). However, these notable economic and recreational benefits directly conflict with conservation goals for native salmonids and other species, making non-native Centrarchidae species a “benefit for anglers but liability for ecosystems” (Carey et al. 2011). This reflects a broader phenomenon in biological invasions, where the benefits and costs of non-native species affect different stakeholders differently and operate over divergent time scales (e.g., temporary costs, permanent benefits), underlining the complexity of invasion outcomes and the importance of intersectoral discourse (Carneiro et al. 2024).

3.7 | Management Strategies for Non-Native Centrarchids

Given their widespread distribution and ecological impacts, non-native centrarchids represent a significant management challenge. Several approaches have been developed to control their spreading populations and mitigate their effects, though with varying degrees of success (Haubrock et al. 2018; Beaune et al. 2019). Management of non-native fish species, such as centrarchids, can involve preventive or direct interventions. Preventive strategies are considered the most cost-effective (Cuthbert et al. 2022), and include legal instruments, such as prohibiting the stocking and release of invasive centrarchids (e.g., pumpkinseed (*L. gibbosus*), which was added to the Union list under EU Regulation 1143/2014 in 2019), as well as public awareness campaigns, for example targeting the angling community (Reniers et al. 2025), since recreational fishing remains one of the main drivers of the introduction of species such as largemouth bass (*M. nigricans*) worldwide (Long and Seguy 2024).

Direct interventions typically focus on mechanical, chemical, or biological strategies. Physical or mechanical removals, such as electrofishing, netting, or draining small reservoirs or ponds, have been applied to reduce or eradicate established populations, sometimes in combination to increase effectiveness (Bosman 2003; Loppnow et al. 2013; Murphy et al. 2015; van Der Walt et al. 2019; Latorre et al. 2025). Electrofishing (as with other physical or mechanical removal methods) is only likely to be effective in shallow, isolated streams and ponds lacking complex

habitat features, such as rocky substrates or dense aquatic vegetation (Loppnow et al. 2013). However, when total eradication cannot be achieved, centrarchid populations tend to recover, especially in highly interconnected systems (Latorre et al. 2025). Chemical control using piscicides such as rotenone can, in some cases, eliminate entire fish assemblages, affecting both native and non-native species, but its long-term effectiveness may be limited (Beamesderfer 2000; Cupp et al. 2020). In river systems, this approach is only effective as a conservation intervention if recolonisation of native species from refuge populations upstream of the treated reach is possible and if barriers to reinvasion are present (Weyl et al. 2014). An alternative and possibly more sustainable management approach in lentic systems is the application of quicklime, a method commonly employed in fish hatcheries. The induced temporary elevation in pH leads to the complete eradication of resident biota, after which the system undergoes a spontaneous ecological reset (Adriaens et al. 2023). Conversely, biological control by introducing native predators (e.g., *Esox lucius*) in ponds with pumpkinseed (*L. gibbosus*) in France showed that predatory pressure was not enough to mitigate the impacts of invasive centrarchids; instead, introduction of biological control agents can modify the invasive potential of these organisms (Beaune et al. 2019).

Centrarchid control efforts may be more efficient when targeting eggs, larvae, and juveniles through techniques that induce nest failure, exploiting the aggressive nest-guarding behaviour of males (e.g., strategic angling, sterilisation) (Loppnow et al. 2013). In Japan, targeting eggs and juveniles in nesting sites to control largemouth bass (*M. nigricans*) populations have shown better results than removing adults (Fujimoto et al. 2021). Also, Japanese researchers are creating sterile males, through gene editing, and releasing them into invaded areas to mate with wild females resulting in reproductive failure, to complement traditional removals (Okamoto et al. 2020). In South Africa, early detection of spotted bass (*M. punctulatus*) allowed for steps that prevented the establishment and spread by placing temporary gabion barriers to physically block upstream movement. This was supplemented with several mechanical removal methodologies leading to total extirpation of spotted bass (*M. punctulatus*) after three years upon introduction (van Der Walt et al. 2019). Total eradication of largemouth bass (*M. nigricans*) was also achieved in ponds by draining and complete drying (Tsunoda et al. 2010).

Another proposed approach in managing non-native centrarchid populations is through habitat restoration (Costantini et al. 2023). Alteration of river flow regimes and reduction of habitat complexity have been shown to influence invasion success of Centrarchidae species (Almeida and Grossman 2014; Choi and Kim 2020). For example, smallmouth bass (*M. dolomieu*) preferred to utilize areas with little to no flow as nesting sites in the Chikuma River, Japan (Peterson et al. 2020). Lentic habitats, such as those created by impoundments, are preferred by introduced largemouth bass (*M. nigricans*) over lotic habitats (Hermoso et al. 2008). Therefore, habitat restoration can deprive these non-native centrarchids of their preferred habitats, potentially reducing their invasion success. Although direct removal measures can be effective under certain circumstances, it is crucial to also implement preventive actions, particularly those aimed at reducing propagule pressure, which may otherwise facilitate the recovery of removed populations.

3.8 | Knowledge Gaps

Our scoping review revealed several knowledge gaps regarding the invasions by non-native Centrarchidae species. First, despite their widespread occurrence on all continents except Antarctica (Figure 5), approximately a third of these species have no documented impacts. This absence of evidence, however, does not mean that these species do not affect the invaded ecosystems, but rather indicates a bias in conducted research or even neglect, as no assessments were identified for most centrarchids. Indeed, of the 30 Centrarchidae species reported as non-native, only ten species were previously assessed, with nine being considered as 'high risk' or 'very high risk'. Considering that species of this family share similar traits, it is plausible that currently unassessed species may pose comparable risks.

Second, previously conducted impact studies primarily focused on ecological consequences and often failed to encompass socio-economic and cultural aspects. Despite this, interactions among non-native centrarchids and with other non-native species remain disproportionately underexplored or underreported. Several ecological aspects, such as parasite–host dynamics, invasion facilitation, and hybridisation warrant further investigation, as these can potentially increase invasion success or amplify both impact and spread potential. Nevertheless, to inform better decisions and formulate effective management actions, assessing socio-economic and cultural impacts is urgently needed, especially since these species are of high economic importance, which increases the likelihood of their introduction.

Lastly, our review highlights recent advances in genomic resources, such as the chromosome-level genome assembly of largemouth bass (*M. nigricans*) (He et al. 2022), which have the potential to greatly enhance our understanding of how non-native species establish, adapt, and spread (e.g., North et al. 2021). Molecular approaches are increasingly revealing key patterns and processes underlying the establishment of centrarchids outside their native range, providing insights into genetic adaptation, population structure and invasion pathways that were previously inaccessible through traditional ecological methods. These molecular approaches can be complemented with other emerging technologies and techniques such as tagging, telemetry, environmental DNA (eDNA), citizen science, and iEcology to increase the capability to track the spread dynamics and invasion fronts of Centrarchidae species (Jarić et al. 2025; Parretti et al. 2023; Meira et al. 2024; Flitcroft et al. 2025).

4 | Conclusions

Centrarchids now constitute a widespread, human-supported invasion complex with clear impact mechanisms, predictable pathways, and mounting ecological risk. Their life-history traits, tolerance to disturbed habitats, and angler- and aquaculture-driven propagule pressure explain their broad establishment and recurrent spread, while taxonomic revisions and frequent hybridisation complicate species determination, detection and control. Impacts are dominated by predation, competition, disease dynamics, and genetic introgression, yet socio-economic and cultural effects remain poorly quantified despite obvious

stakeholder trade-offs. Our SDMs and case studies indicate that warming, impoundment, and continued stocking will open new fronts, expanding risk poleward and upstream unless propagule pressure is cut. Although most species have not been introduced beyond North America—and Australia remains without centrarchids—further research on their invasion ecology is needed to anticipate emerging threats. Management should prioritize prevention and pathway control, rapid response keyed to nests and early life stages, and long-term habitat restoration that reduces lentic refugia, with eradication pursued only where re-invasion can be blocked. Two investments would unlock faster progress: (i) harmonised, multi-framework risk screening across all centrarchid species and regions, and (ii) genomic surveillance to resolve identities, introduction sources, and hybridisation patterns. Collectively, these actions could transform a fragmented evidence base into actionable guidance for balancing fisheries benefits with the protection of native biodiversity.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this study is available in public databases (e.g., GFID, GRISS, GBIF) and the provided [Supporting Information](#).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** List of published papers included in the review. **Data S2:** In the following, a few well known non-native Centrarchidae are described, pointing towards their current distribution and suitable habitat. **Figure S1:** Density map of the global distribution of the non-native Centrarchidae (based on the *Global Biodiversity Information Facility* (GBIF; GBIF.org 2025)) and extracted using the rgbif R package (Chamberlain et al. 2022). Note that this map does not include the native occurrences in North America (see Figure 3) and occurrences in North America, which are difficult to ascertain at finer scales. **Table S1:** Summary of the search strings used to gather the publications for native and non-native Centrarchidae species (TS—Topic Search). **Table S2:** Overview of pathway categories, subcategories, and intentionality components used to classify non-native Centrarchidae species introductions following the CBD framework (Harrower et al. 2018; Saul et al. 2017). **Table S3:** Results of Aquatic Species Invasiveness Screening Kit (AS-ISK) assessments for Centrarchidae species across different regions. Scores are reported as Basic Risk Assessments (BRA) and BRA combined with Climate Change Assessment (BRA+CCA). Risk outcomes for the BRA are based on the global threshold of 14.7 ("Low" for –20 to 1, "Medium" for 1 to 14.7 and "High" for > 14.7) and for the BRA + CCA on a threshold of 17.7 ("Low" for –32 to 1, "Medium" for 1 to 17.7 and "High" for > 17.7). **Table S4:** Area under the curve (AUC) **Table S5:** List of known non-native Centrarchidae species and countries where they are labelled as "invasive". Data extracted from GRIIS Invasive Species Specialist Group database.