Global patterns of fish–macrocrustacean interactions in freshwater environments: a systematic review

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ABSTRACT

1. Understanding species interactions is central to ecology, yet they remain one of the least documented dimensions of biodiversity (the Eltonian shortfall). Most studies have focused on terrestrial vertebrates, while aquatic vertebrates and invertebrates are still poorly understood. Here, we assessed broad patterns in the published literature on

interactions between fishes and macrocrustaceans in freshwater ecosystems, identifying the main interaction types, habitat, and major geographical and taxonomic gaps.

2. We conducted a systematic literature review using the Scopus database, including articles published up to December 2025, and identified 96 eligible studies conducted in freshwater environments. We classified studies according to interaction type, habitat, country and taxonomic group, and quantified research effort through number of publications.
3. The retrieved literature focused primarily on predation, followed by parasitism, competition, and commensalism, and was conducted mainly in streams, lakes and rivers, whereas wetlands were markedly underrepresented. In absolute terms, studies were concentrated in the United States, Brazil, and Canada. When publication counts were standardised by national land area, the highest values were recorded for Trinidad and Tobago, Puerto Rico, and Czechia. Most studies involved native fishes and native macrocrustaceans, although interactions between native fishes and non-native macrocrustaceans formed the second most frequent category.
4. These patterns may reflect historical, methodological, and ecological biases, including the predominance of trophic approaches, the greater practical accessibility (e.g., logistical issues) of certain habitats, and the influence of established model systems.
5. Our results highlight a pronounced Eltonian shortfall in freshwater ecosystems. Expanding research across neglected habitats, interaction types, and taxa, as well as conducting more direct field observation studies, will be essential to improve our understanding of biodiversity interaction dynamics and predictions of ecological responses to global environmental change.

Keywords: Biological invasions, commensalism, competition, Eltonian shortfall, parasitism, predation.

INTRODUCTION

One of the most critical gaps in biodiversity science concerns the understanding of interactions between species (i.e., the Eltonian shortfall; Hortal et al. 2015). The Eltonian shortfall is a major barrier to our capacity to understand the outcomes of global change, as interaction strengths between ecological components drives community structure (Galiana and Araújo 2026). Species responses to a rapid environmental change are mediated not only by abiotic tolerances to their environment, but also by interspecific interactions (and their magnitudes) that modulate community structure and ecosystem functioning (Åkesson et al. 2021). Freshwater ecosystems are one of the most vulnerable to biodiversity loss (Haase et al. 2023). In the freshwater context, resolving aspects of the Eltonian shortfall becomes even more urgent, since these environments support a disproportionate share of global biodiversity and, at the same time, are subjected to intense anthropogenic pressures (Sayer et al. 2025) and climate change (Tonkin et al. 2026). Recent assessments indicate that approximately one quarter of freshwater fauna is threatened with extinction due to pollution, habitat fragmentation, and the introduction of non-native species (Sayer et al. 2025). Investigating species interactions is essential to establish a baseline understanding of freshwater communities, particularly as these threats and climate change drives range shifts and generates novel biotic interactions (Antão et al. 2020; Thurman et al. 2020; Windsor 2023). Without this foundation, detecting and interpreting ecological change becomes inherently limited (Windsor 2023).

Interactions between fishes and macrocrustaceans (e.g., Palaemonidae mutilating Gobiidae in streams; see Sabino 1995) are particularly relevant because of both their ecological roles and their importance for human livelihoods and food security (Tejeda-Mazariegos et al. 2018; Funge-Smith and Bennett 2019). Fishes are important components of freshwater ecosystems, occupying central positions in freshwater food webs, functioning as predators,

79 competitors, omnivores and consumers across multiple trophic levels (Lee et al. 2022), but also
80 participating in biogeochemical cycles and functioning as environmental engineers (e.g.
81 Pelicice et al. 2023), being important seed dispersers, for example (see Correa et al. 2025). On
82 the other hand, freshwater macrocrustaceans play fundamental ecological roles, especially in
83 detritus processing, nutrient cycling, bioturbation, and trophic regulation (Gherardi 2007; Silva
84 et al. 2020). Crustacean decapods, such as crayfish and crabs, can also act as active predators,
85 whereby in some systems, these taxa can dominate secondary production and biomass
86 (Gherardi 2007; Reynolds and Souty-Grosset 2011). In addition to their ecological roles,
87 decapod crustaceans have great socioeconomic relevance as food resources, representing
88 approximately 22% of the value of global trade in aquatic animal products (FAO 2026).
89 Thus, interactions between these groups are not limited to unidirectional predator-prey
90 relationships, but may also involve competition for food and shelter, behavioural interference,
91 habitat-mediated effects, and indirect consequences at the community level (Reynolds 2011).
92 For example, predation risk from fishes generates non-consumptive effects that regulate shrimp
93 habitat use in tropical streams through landscape-of-fear effects, in addition to direct predation
94 (Silva et al. 2020). Similarly, the risk of predation by fishes alters crayfish habitat use, leading
95 individuals to preferentially occupy shallow waters where predation risk is lower (Englund and
96 Krupa 2000). Characterising the interactions between these taxa provides an opportunity to
97 better understand the complex effects of global change at the interaction level rather than at the
98 level of individual species (Windsor 2023; Teichert et al. 2025).
99 In this context, our study aims to investigate the global patterns on interactions between
100 macrocrustaceans and fishes in freshwater systems. Specifically, we quantify how the studies
101 are distributed among interaction types (e.g., predation, competition, parasitism, and
102 commensalism), and evaluate how studies are distributed across freshwater habitats and
103 geographic regions, considering both absolute publication counts and publication counts

104 standardised by national land area (Costa et al. 2025). We further examine the number and
105 structure of interaction links between fish and macrocrustacean families for each interaction
106 type, and compare the number of studies concerning at least one non-native taxon with those
107 regarding only native taxa to identify taxonomic and ecological biases in current knowledge.
108 We hypothesise that predation dominates the literature, largely due to the relative ease in
109 documenting such interactions compared to mutualism, competition and commensalism. Thus,
110 reflecting the prevailing view of fish-macrocrustacean relationships as primarily unidirectional
111 trophic interactions, despite evidence of more complex dynamics (Mason and Evans 2011). By
112 synthesising these patterns, we aim to provide a comprehensive global overview of these
113 interactions, but also to highlight critical knowledge gaps and stimulate research on
114 underexplored interaction types, particularly in the face of ongoing environmental change.
115

116 **METHODS**

117 **Data collection**

118 In March 2026, we conducted a literature review using the Scopus database, including
119 articles published up to December 2025. We selected Scopus due to its broader journal
120 coverage compared to other databases, such as Web of Science (Mongeon and Paul-Hus 2016).
121 Its extensive international coverage and advanced search functionality also facilitate
122 transparent and reproducible literature searches, making it suitable for the objectives of this
123 bibliographic synthesis. We searched article titles, abstracts, and keywords using predefined
124 Boolean search strings (see Figure 1).
125

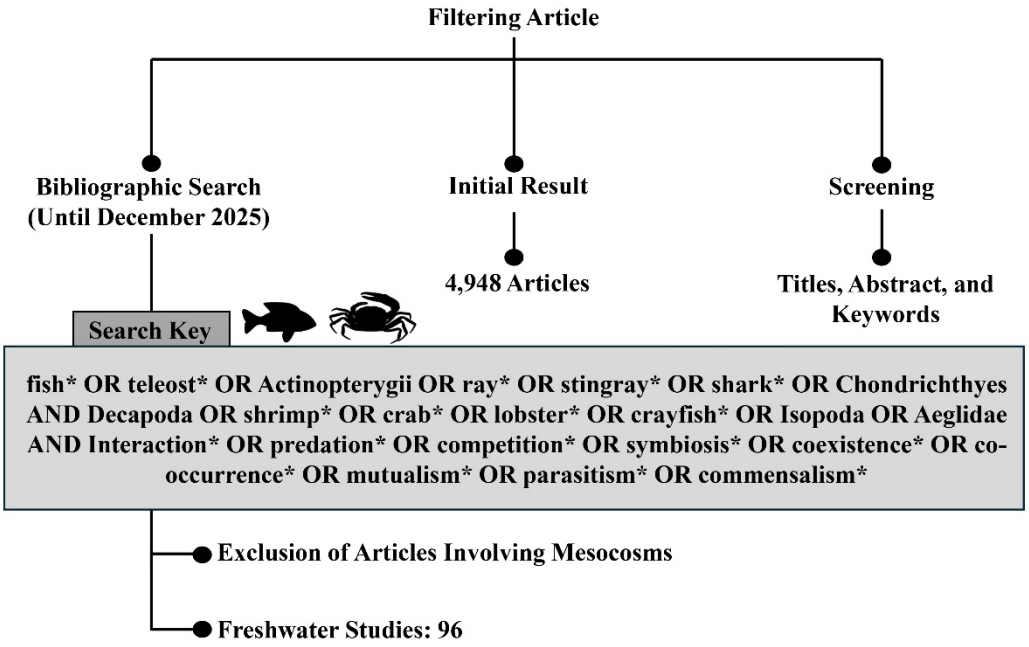

Figure 1. Schematic representation of the article filtering process used in this review. The bibliographic search was conducted in the Scopus database up to December 2025, using terms related to fish, crustaceans, and their ecological interactions.

Inclusion criteria

Studies were included when they met all the following criteria: (i) they were published as peer-reviewed articles or short notes; (ii) they investigated ecological interactions between freshwater fishes and macrocrustaceans; and (iii) they were written in English or provided at least an English-language title and abstract.

Titles and abstracts were screened independently by two reviewers. Potentially eligible articles were subsequently assessed in full text, and disagreements were resolved through discussion with a third reviewer.

Exclusion criteria

Our initial search returned 4,948 records, which were subsequently filtered by document type. Books, book chapters, conference papers, conference reviews, data papers, editorials, errata, letters, reviews, and other non-peer-reviewed publications were excluded.

We also excluded studies focusing exclusively on fishes or macrocrustaceans interactions with other taxonomic groups, studies addressing only fishes or macrocrustaceans, and studies involving microcrustaceans rather than macrocrustaceans. Studies based solely on dietary descriptions, in which one taxon was reported merely as a food item without explicitly investigating the interaction between fishes and macrocrustaceans, were also excluded.

The remaining studies were then examined individually to confirm their eligibility for inclusion in the final dataset. Only studies that specifically investigated interactions between fishes and macrocrustaceans were retained. Macrocrustaceans were defined as non-planktonic eumalacostracean crustaceans considered one of the focal taxa in interactions and occurring within natural freshwater environments, even when these interactions were not the primary focus of the study.

Studies containing only mesocosms or aquarium tanks were removed, but studies combining laboratory experiments with field observations or field experiments were retained. Studies investigating fish–macrocrustacean interactions using approaches other than direct underwater observation were also retained, including fisheries time-series data, stable isotope analyses, community sampling, and nest sampling.

Final dataset

After this filtering process, we identified 96 studies conducted with fish-macrocrustacean interactions in freshwater systems, which were included in the final dataset

(Figure 1). The complete list of studies is provided in the Data Availability Statement and Table S1.

Data extraction

For these 96 studies, we extracted information on year of publication and interaction type, classified into four categories: competition, predation, parasitism, and commensalism. We also recorded the type of freshwater environment, the country where the study was conducted, and the fish and macrocrustacean families involved. For predation studies, we further classified the direction of the interaction (i.e., whether fishes preyed on macrocrustaceans or the opposite). We also classified the fish and macrocrustacean families involved according to their biogeographic status (native or non-native). Taxa were considered non-native whenever the original study described them as non-native, invasive, or introduced.

Data analysis

For each interaction type, we analysed temporal trends using cumulative numbers of studies per year. We then summarised the frequency of studies across habitat types and mapped the geographic distribution of research effort by country for competition, predation, and parasitism (commensalism was not mapped because only a single study, conducted in Brazil, was available). For this purpose, considering each interaction type, we used two metrics in global maps: one showing the total number of studies and another showing the number of studies per million km^2 (country land area-standardised publication counts).

To describe taxonomic patterns of interaction networks in freshwater systems, we summarized links between fish and macrocrustacean families or assemblages for each interaction type. For predation, links were analysed separately according to whether fish or macrocrustaceans acted as predators. The number of links between taxa was visualised using

Sankey diagrams, with link width proportional to the number of studies. Diagrams were produced using the *networkD3* package (Allaire et al. 2025).

Each study was classified into one of four categories according to the native or non-native status of fishes and macrocrustaceans: (*i*) native fish × native macrocrustacean, (*ii*) native fish × non-native macrocrustacean, (*iii*) non-native fish × native macrocrustacean, and (*iv*) non-native fish × non-native macrocrustacean. The number of studies in each category was then summarized and partitioned by interaction type (competition, predation, parasitism, and commensalism) using a stacked bar chart. To test whether studies involving at least one exotic taxon were more frequently represented than studies involving only native taxa, we created a binary variable indicating the presence (1) or absence (0) of at least one exotic taxon in each study and performed an exact binomial test against an expected proportion of 0.5. All Statistical analyses and figures were produced in R version 4.4.3 (R Core Team 2026).

RESULTS

We identified a total of 96 articles, with the number of studies on fish–macrocrustacean interactions varying markedly among interaction types (Figure 2A). Predation was the interaction type with the largest number of studies (67; 69.8%), followed by parasitism (16; 16.66%), competition (12; 12.5%), and commensalism (1; 1.04%). Predation studies showed the longest temporal record and accumulated more rapidly over recent decades, particularly from the late 20th century onwards, tending to increase in recent decades. Despite this, parasitism and competition also showed an increasing trend (although less pronounced for competition), even though the first studies found for these interaction types began around the year 2000 (Figure 2B). On the other hand, a single study for commensalism was identified, published in 2014. Studies on fish–macrocrustacean interactions were conducted across a variety of freshwater environments (Table 1). Among the 98 environmental records obtained

(two studies encompassed more than one habitat category), streams were the most frequently represented environments (35.7%), followed by lakes (29.6%) and rivers (23.5%), whereas ponds, reservoirs, wetlands, and subterranean cave systems were comparatively less represented.

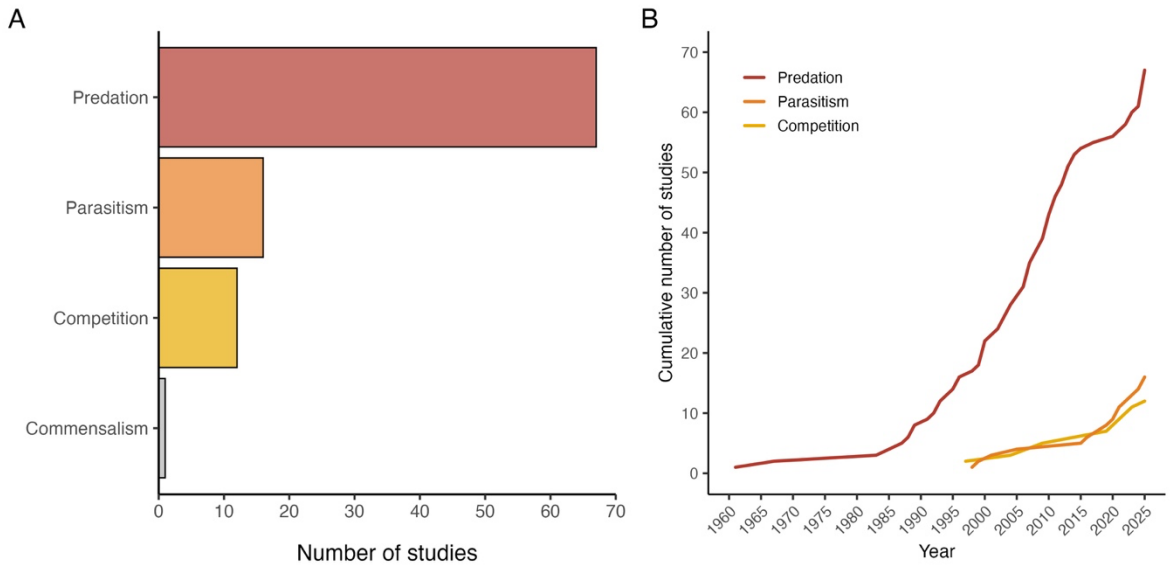

Figure 2. Global patterns of studies on fish–macrocrustacean interactions in freshwater environments. (A) Number of studies by interaction type (competition, predation, parasitism, and commensalism). (B) Temporal trends showing the cumulative number of studies over time for three major interaction types: predation, parasitism, competition. Commensalism was not included because only a single published study was identified.

234 **Table 1.** Summary of studies on macrocrustacean-fish interactions **(A)** in different freshwater
235 environments **(B)**.

(A)		
Types of Interactions Between Fish and Macrocrustaceans	**Number of Studies (n)**	**Percentage (%)**
Predation	67	69.8
Parasitism	16	16.66
Competition	12	12.5
Commensalism	1	1.04
Total	**96**	**100**
(B)		
Types of Freshwater Environment	**Number of Studies (n)**	**Percentage (%)**
Stream	35*	35.7
Lakes	29*	29.6
Rivers	23*	23.5
Ponds (Aquaculture or Urban)	4	4.0
Reservoirs	3*	3.1
Wetlands	3	3.1
Cave/ Subterranean Freshwater Systems	1	1.0
Total	**98**	**100**

236 ***** Two studies were counted in more than one environmental category because they simultaneously assessed
237 lakes and rivers, streams and reservoirs, respectively.
238

239 Globally, studies on competition were concentrated in the Northern Hemisphere,
240 particularly in North America and Europe (Figure 3). In contrast, predation studies were more
241 widely distributed across all continents, although North America accounted for the highest
242 number of studies (Figure 3). Parasitism showed a relatively broad and more even global
243 distribution (Figure 3). The countries with the highest number of total studies (considering all
244 interaction types) were respectively the United States (39 studies), Brazil (7), and Canada (4).
245 When considering the number of studies divided by country land area, competition studies
246 remained concentrated in North America and Europe, reflecting the limited geographical
247 distribution of competition studies (Figure S1). Predation studies retained a broader
248 geographical distribution, although the relative prominence of the United States decreased after
249 area standardisation. A similar pattern was observed for parasitism. Across all interaction types,
250 Trinidad and Tobago, Puerto Rico, and Czechia had the highest numbers of studies per million
251 km^2.

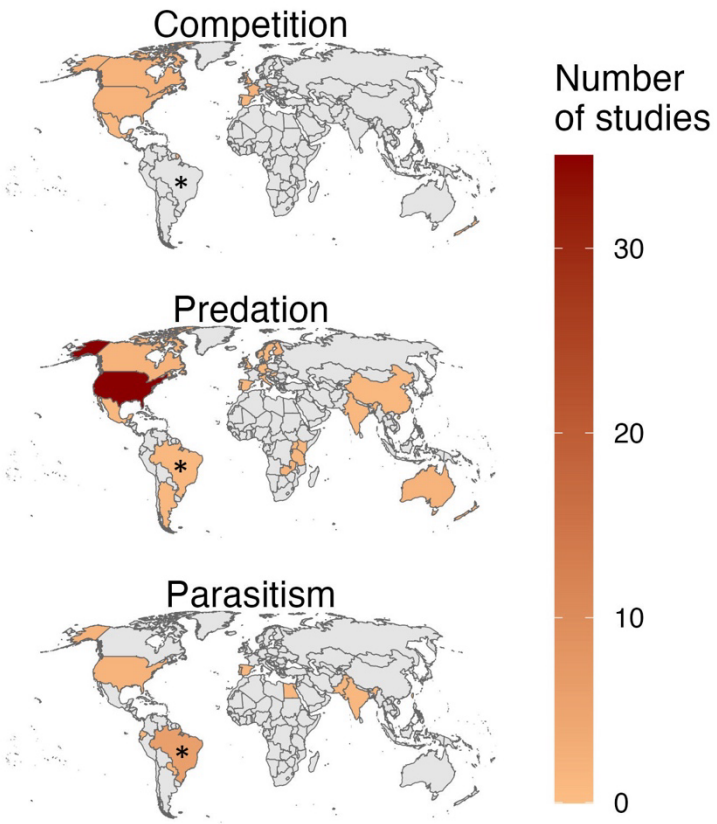

Figure 3. Global distribution of studies on macrocrustacean-fish interactions in freshwater environments by interaction type: competition, predation, and parasitism. Color intensity represents the number of studies per country. The asterisk in the maps indicates the only article dealing with commensalism involving fish and macrocrustaceans, registered for Brazil.

Across all interaction types, studies most frequently examined fishes at the assemblage level (n = 26; 27.4%), whereas Salmonidae was the most frequently represented fish family (n = 15; 15.8%), followed by Centrarchidae (n = 9; 9.5%) and Percidae (n = 8; 8.4%) (Table 2A). Among macrocrustacean families, Cambaridae was markedly predominant (n = 40; 42.1%), followed by Cymothoidae (n = 12; 12.6%), Astacidae (n = 9; 9.5%), and Atyidae (n = 7; 7.4%) (Table 2B).

266 **Table 2**. Summary of fish (A) and macrocrustacean (B) assemblages recorded in studies
267 addressing their interactions in freshwater environments.

(A) Taxonomic Unit	Number of Studies (n)	Percentage (%)
Assemblage*	26	27.1
Salmonidae	15	15.6
Centrarchidae	9	9.4
Percidae	8	8.3
Cyprinidae	5	5.2
Poeciliidae	4	4.2
Ictaluridae	3	3.1
Cichlidae	2	2.1
Gasterosteidae	2	2.1
Loricariidae	2	2.1
Latidae	2	2.1
Synbranchidae	2	2.1
Acestrorhamphidae	1	1.0
Acipenseridae	1	1.0
Anguillidae	1	1.0
Characidae	1	1.0
Clupeidae	1	1.0
Cottidae	1	1.0
Curimatidae	1	1.0
Engraulidae	1	1.0
Esocidae	1	1.0
Fundulidae	1	1.0
Leucisidae	1	1.0
Mugilidae	1	1.0
Nemacheilidae	1	1.0
Notoperidae	1	1.0
Petromyzontidae	1	1.0
Potamotrygonidae	1	1.0
Total	**96**	**100**

(B) Taxonomic Unit	Number of Studies (n)	Percentage (%)
Cambaridae	40	41.7
Cymothoidae	12	12.5
Astacidae	9	9.4
Atyidae	7	7.3
Palaemonidae	5	5.2
Parastacidae	5	5.2
Assemblage*	4	4.2
Mysidae	4	4.2
Isopoda*	3	3.1
Asellidae	2	2.1
Aegidae	1	1.0
Aeglidae	1	1.0
Shrimp*	1	1.0
Trichodactylidae	1	1.0
Xiphocaridae	1	1.0
Total	**96**	**100**

268 * Taxa were classified at the family level whenever possible. When studies reported organisms only at broader
269 taxonomic levels, the lowest available taxonomic classification was retained. The category assemblage was used
270 when multiple fish or macrocrustacean groups were analysed jointly in the original study.
271
272

Competition studies comprised nine distinct interaction links, with most studies examining fish assemblages interacting with multiple macrocrustacean families or assemblages (Figure 4A). For parasitism, 12 interaction links were identified, with Cymothoidae being the most studied parasite family, primarily associated with fish assemblages (Figure 4B). For predation with fishes as predators, 28 interaction links were identified. Despite the diversity of interactions, research was largely concentrated on fish assemblages, Centrarchidae, and Salmonidae, preying predominantly on Cambaridae (Figure 5A). For crustaceans acting as predators, 10 links were recorded, with most studies focusing on Cambaridae preying upon multiple fish families and on Palaemonidae preying on Poeciliidae (Figure 5B). The only commensalism study reported an interaction between Potamotrygonidae (a stingray) and Palaemonidae.

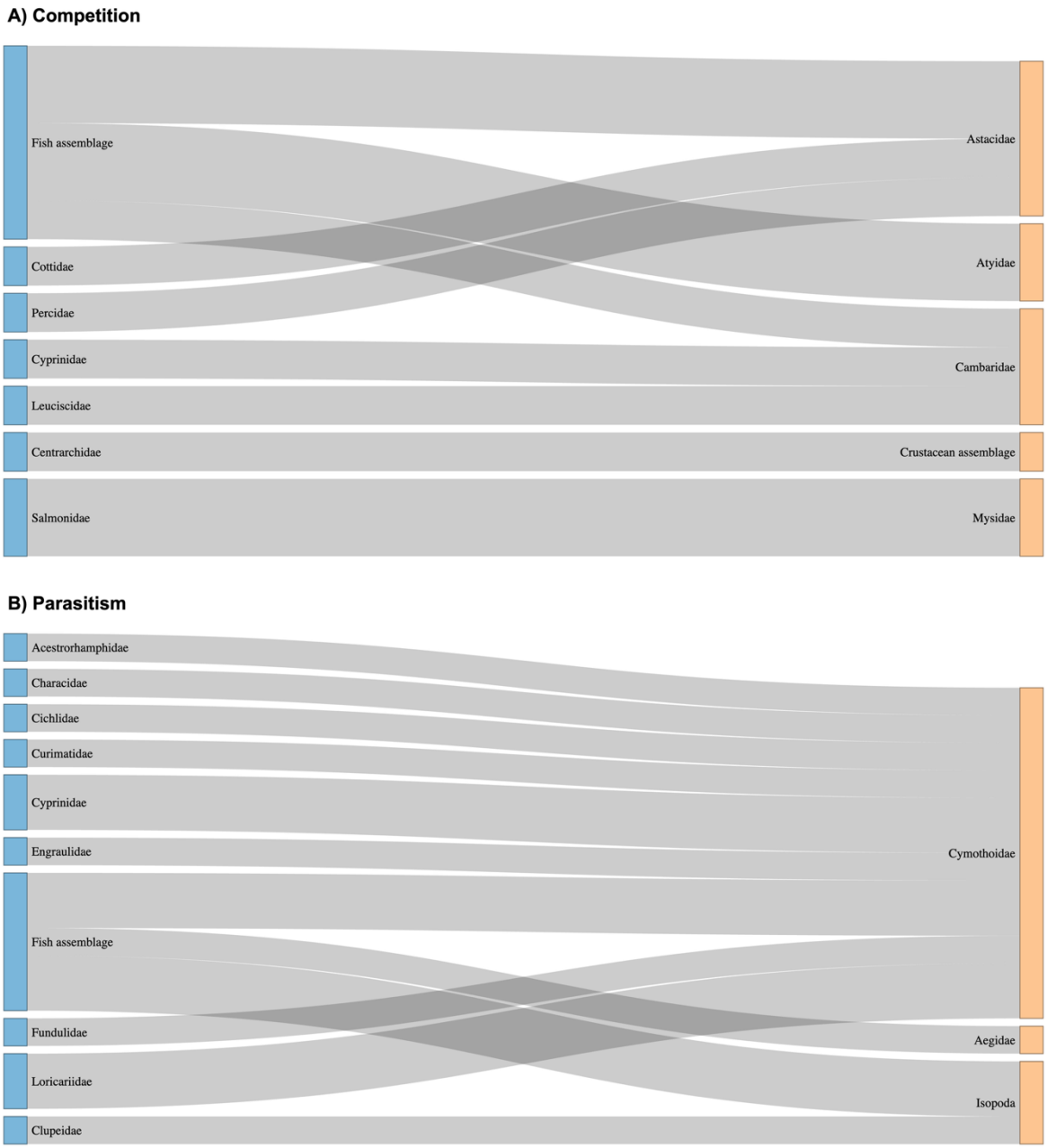

Figure 4. Sankey diagram illustrating interactions between fish and macrocrustacean families (or assemblages) in freshwater systems, for (A) competition and (B) parasitism. Links represent recorded interactions between fish (blue) and crustaceans (orange), with link width proportional to the number of studies. “Isopoda” appears when the family was not specified in the study.

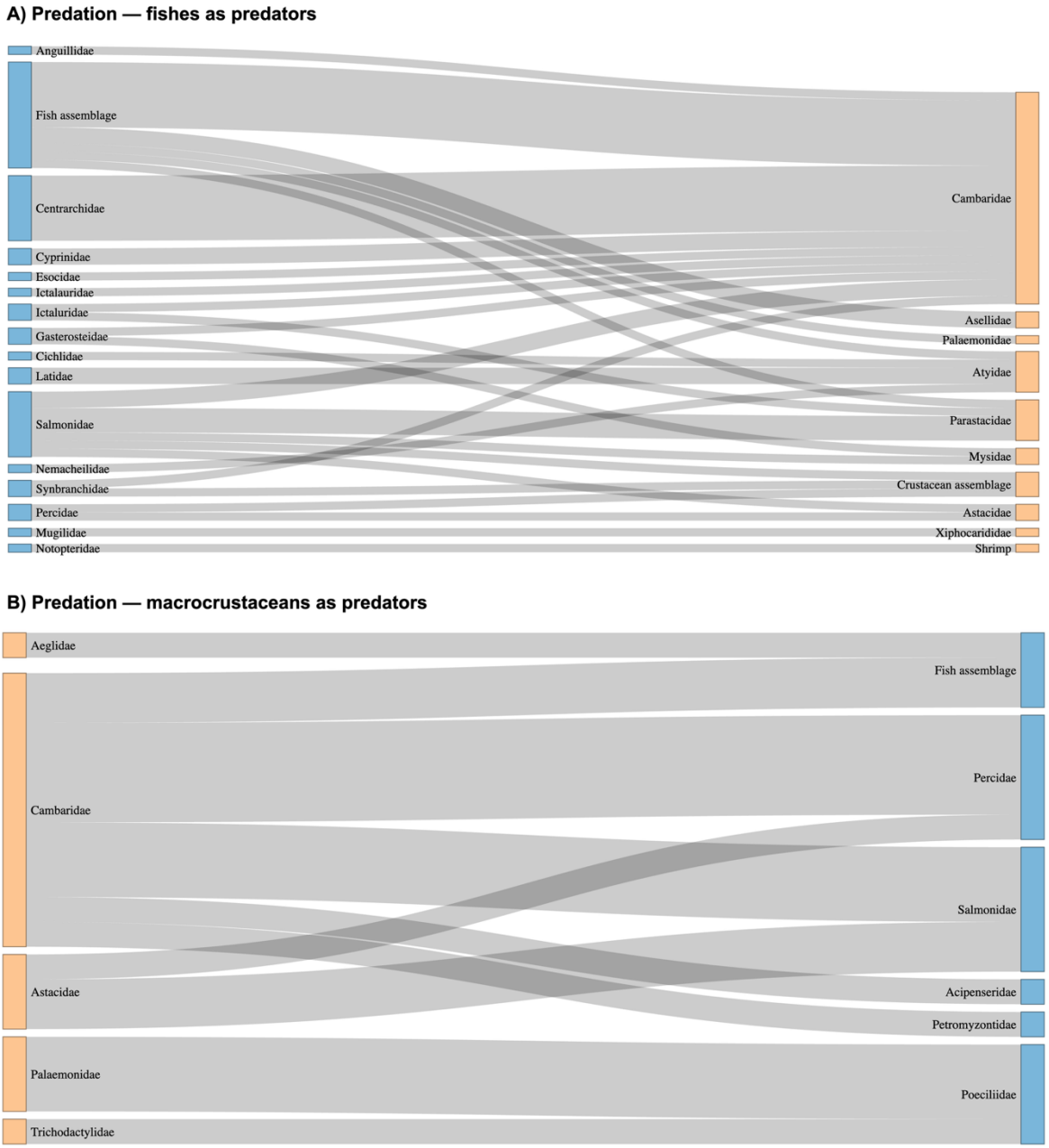

Figure 5. Sankey diagram illustrating interactions between fish and macrocrustacean families (or assemblages) in freshwater systems, for predation with (A) fishes as predators and (B) macrocrustaceans as predators. Links represent recorded interactions between fish (blue) and crustaceans (orange), with link width proportional to the number of studies. “Shrimp” appears when the study did not mention the taxon name.

Most studies involved interactions between native fish and native macrocrustacean taxa (n = 60), followed by studies involving native fish and non-native macrocrustaceans (n = 27), non-native fish and native macrocrustaceans (n = 6), and both non-native taxa (n = 3) (Figure 6). Predation accounted for the majority of studies across all categories. Overall, 37.9% of studies involved at least one non-native taxon, whereas 62.5% involved only native taxa. The proportion of studies involving non-native taxa was significantly lower than expected under an equal representation of native-only and non-native-associated studies (Exact Binomial Test: p = 0.018; 95% CI = 0.278–0.479).

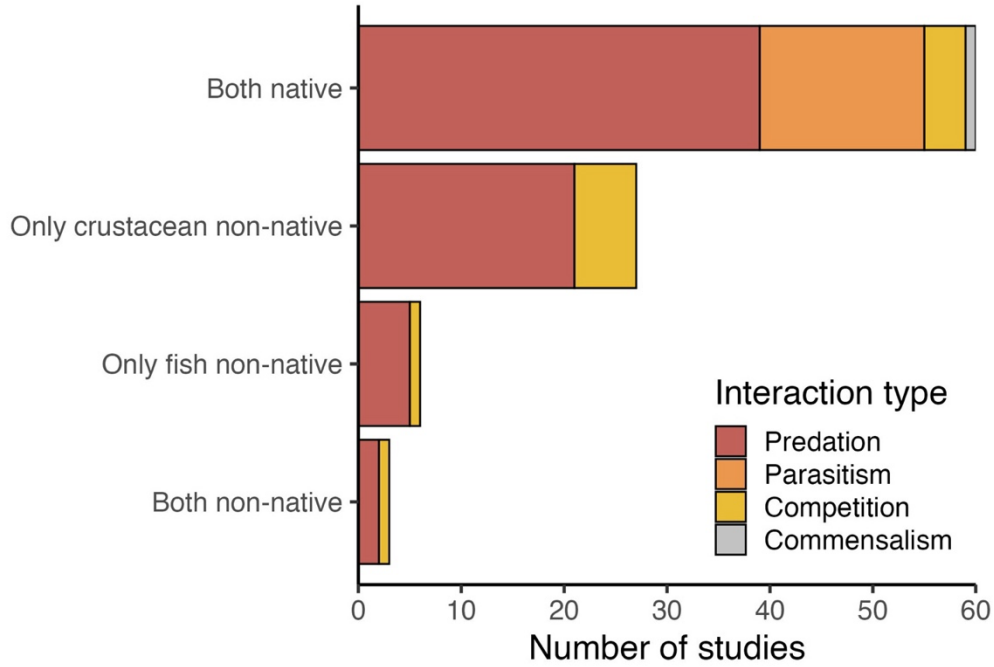

Figure 6. Number of studies involving native and non-native fish and macrocrustacean taxa across different interaction types. Studies were classified into four categories according to the origin status of the interacting taxa (native or non-native).

DISCUSSION

Our results revealed a surprisingly small body of literature on freshwater fish-macrocrustacean interactions in natural environments, with only 96 studies identified worldwide despite the ecological importance and broad geographic distribution of both groups. This finding highlights a potentially large Eltonian shortfall, whereby species interactions remain substantially less documented than species occurrences and distributions (Hortal et al. 2015). Given the high diversity of freshwater fishes and macrocrustaceans, together with their central roles in food webs, nutrient cycling, and ecosystem functioning, the low number of studies suggests that interactions between these taxa have received relatively little attention from freshwater ecologists. One possible explanation is the logistical difficulty of studying interactions directly in aquatic environments, particularly in freshwaters. Many interactions require labour-intensive field observations, underwater surveys, manipulative field experiments, or long-term monitoring data to be reliably detected (e.g., Sabino 1995; Garrone-Neto et al. 2014; Hyatt et al. 2021). This gap is especially concerning given that freshwater ecosystems are among the most threatened environments worldwide and are increasingly experiencing biological invasions, habitat alteration, and climate-driven shifts that can generate novel ecological interactions or the loss of interactions even before they are described, due to species extinction or population extirpations (Antão et al. 2020; Windsor 2023).

Predation was the predominant interaction type, accounting for nearly 70% of all studies identified in our review. This pattern supports our hypothesis that fish-macrocrustacean interactions are predominantly investigated from a trophic perspective. Although competition and parasitism have received increasing attention in recent decades, they remain considerably less represented in the literature. The strong focus on predation suggests that other interaction types are likely underexplored, contributing to the Eltonian shortfall in freshwater ecosystems. This pattern is particularly evident for commensalism, for which we identified only a single

study worldwide (Garrone-Neto et al. 2014). That study reported a cleaning interaction between the palaemonid shrimp *Macrobrachium jelskii* (Miers, 1878) and the freshwater stingray *Potamotrygon falkneri* Castex and Maciel, 1963 in the Paraná River, Brazil. The shrimps fed on mucus and dead tissue from the stingray's body, whereas no clear benefit to the host was detected. Interestingly, this interaction involved a fish species that commonly consumes palaemonid shrimps (Garrone-Neto et al. 2014), suggesting that particular environmental or behavioural conditions may facilitate unexpected and rarely documented ecological interactions in freshwater ecosystems.

Similarly, unusual interactions may be overlooked even when they clearly involve fishes and macrocrustaceans. For example, Dominey and Snyder (1988) documented kleptoparasitism by cichlids in Lake Barombi Mbo, Cameroon, which followed freshwater crabs and stole prey items exposed during their foraging activities. Likewise, Sabino (1995) described freshwater shrimps actively attacking live fishes and feeding on their fins and body tissues without immediately killing them. Neither study was retrieved by our search strategy, probably because the interactions were framed using specific terms such as "kleptoparasitism" and "mutilation" rather than the broader categories included in our search strings (e.g., competition or predation). Although this represents a limitation of our review, it also illustrates how unconventional interactions may remain underrepresented in syntheses of ecological interactions, suggesting that the Eltonian shortfall for freshwater ecosystems may be even greater than currently recognized. Moreover, the scarcity of direct observational studies of the natural history and behavior of aquatic animals in freshwaters may strongly impair the discovery of possibly remarkable biological interactions, which can be pivotal for generating new ecological hypotheses (Willson and Armesto 2006; Wilson 2017).

The number of studies was unevenly distributed among habitat types, with streams, lakes, and rivers accounting for the majority of environmental records. This pattern may partly

366 reflect the historical development of freshwater ecology, which has traditionally focused on
367 these systems as central model environments (Allan and Castillo 2007), and they are also the
368 primary environment type studied for other topics related to freshwater fauna (Faghihinia et al.
369 2021; Gomes et al. 2023). In contrast, wetlands were markedly underrepresented despite their
370 recognised ecological importance. Similar biases have been reported across several areas of
371 ecological research and are concerning because wetlands can support high levels of
372 biodiversity and endemism (Yoezer et al. 2026) and harbour numerous threatened freshwater
373 taxa (Sayer et al. 2025). Wetlands are also economically and socially important because they
374 support fisheries, food provision and local livelihoods (Singha and Pal 2023). Their limited
375 representation in our dataset is therefore more likely to reflect a research bias than an absence
376 of fish–macrocrustacean interactions or a low richness and abundance of the taxa involved.
377 This relative underrepresentation in the literature may be partly explained by the high spatial
378 and temporal variability of wetlands, which can complicate sampling design, field access, and
379 methodological standardisation. Habitat-related biases may also overlap with geographic
380 biases, because several important African wetlands support both native freshwater crabs and
381 populations of non-native crustaceans, yet information on their ecological roles – and possible
382 biological interactions - remains limited (Madzivanzira et al. 2021a; Nawa et al. 2024; Nawa
383 et al. 2026).

384 Burrowing crayfish present an additional challenge when assessing fish-
385 macrocrustacean interactions in wetland and transitional environments. Although these
386 organisms are generally regarded as freshwater taxa because of their phylogenetic affinities
387 and dependence on moist environments, many primary burrowers spend substantial periods in
388 subterranean or semi-terrestrial burrow systems, sometimes far from permanent surface waters
389 (Bloomer et al. 2021). Therefore, their interactions with fishes may be restricted to specific
390 hydrological conditions, such as flooding or temporary connections with permanent aquatic

habitats. These interactions can be difficult to observe and may fall near the boundaries of the eligibility criteria adopted in this review. Their weak representation is largely due to methodological difficulties rather than an inherent ecological implication. These gaps are particularly concerning as they limit our understanding of species interactions in ecologically critical and highly vulnerable systems, reinforcing the need for greater research attention in wetland habitats.

The national-level patterns indicate that absolute and normalized metrics capture different dimensions of scientific output. The predominance of countries such as the United States, Brazil, and Canada in absolute numbers is consistent with their large research systems, extensive territories and substantial availability of freshwater habitats. By contrast, the number of studies per million km² reflect the relative intensity of this effort in relation to the territorial size of each country, and not just its absolute scientific output. Small countries or territories such as Trinidad and Tobago, may present a modest contribution in absolute terms but gain prominence when the data are relativized, especially for studies on parasitism and predation (European Commission 2024). Nevertheless, the prominence of particular countries may partly reflect the regional importance of well-established biological models, including *Poecilia* species in Trinidad and Tobago (Bassar et al. 2010).

Studies on competition did not follow this same pattern, but were concentrated more strongly in the Northern Hemisphere, particularly in Europe and North America. This result suggests that geographical distribution of records of this interaction type may be influenced not only by differences in scientific output capacity between countries, but also by the ecological contexts and regional research biases. In Europe, for example, considerable attention has been directed towards the ecological consequences of biological invasions, particularly those involving non-native crayfish species. Interactions between introduced crayfish and native fishes may involve competition for food, shelter, and habitat, although the strength and

direction of these interactions can vary among systems (Reynolds 2011; O'Hea-Miller et al. 2024). Substantial dietary overlap between invasive signal crayfish and native fishes has, for example, been documented in Iberian rivers (Vedia et al. 2019).

When considering studies involving predation, a predominance of some taxonomic groups stands out in scientific production, which can also be explained by research biases, as well as the regional ecological/biogeographical context. Salmonidae and Centrarchidae appear as the most frequently represented fish families, whereas Cambaridae dominated among macrocrustaceans. Studies have focused on salmonids such as *Salmo trutta* Linnaeus, 1758 preying on non-native crayfish (Matos et al. 2025), whereas centrarchids have been investigated as important predators of juvenile crayfish capable of influencing crayfish distribution patterns in stream ecosystems (Fortino and Creed 2007). These patterns reflect the historical relevance of models adopting these organisms in freshwater ecology research, particularly in North America (Reynolds 2011; Hansen et al. 2013; Matos et al. 2025). This predominance of certain groups reinforces the idea that studies on predation, as well as interactions between freshwater fish and macrocrustaceans, are strongly influenced by regional biases or established study models, while many other family combinations are poorly represented or entirely absent. Thus, it is likely that large gaps still exist for numerous lineages of freshwater fish and macrocrustaceans, especially since many studies focus on only a single species within a family.

The predominance of the Cambaridae among macrocrustaceans reflects once again the central role of these individuals in ecological systems and freshwater food webs, because several cambarid species have expanded beyond their native ranges and became abundant in recipient ecosystems, where they are consumed by fishes while also acting as predators themselves (O'Hea-Miller et al. 2024). In North America, interactions between centrarchids and crayfish represent a well-established model of predation in freshwater habitats (Tetzlaff et

441 al. 2011; Hansen et al. 2013), with predatory fish potentially acting as top-down regulators of
442 non-native crayfish populations (Hansen et al. 2013). Conversely, non-native Cambaridae and
443 Parastacidae can prey upon fishes, by consuming eggs, larvae, or other early life stages (Morse
444 et al. 2013; Crossman et al. 2018; Madzivanzira et al. 2021b). These contrasting roles reinforce
445 the bidirectional nature of predation between fishes and crayfish in invaded systems, as well as
446 the relevance of macrocrustaceans as predators in freshwater ecosystems.

447 The interaction networks detected in our study also indicate that macrocrustaceans can
448 function as active predators of fishes beyond crayfish-based models. For example, some
449 palaemonid shrimps have been reported capturing poeciliid fishes (McKellar et al. 2009;
450 McKellar and Hendry 2011), and aeglids have been reported preying on fish in opportunistic
451 conditions (Savaris et al. 2012). The only record involving brachyuran crabs in our review was
452 provided by Klaus and Plath (2011), who documented predation on the cave fish *Poecilia*
453 *mexicana* by the freshwater crab *Avotrichodactylus bidens* in a Mexican sulfidic cave. This
454 record is particularly relevant because empirical studies focusing on fish predation by
455 freshwater crabs are rare, and the authors suggest that *A. bidens* may act as a top predator in
456 this subterranean ecosystem. Additionally, experimental data on freshwater crab
457 (Potamonautidae) potential to predate fish fry was not picked up by our review (Madzivanzira
458 et al. 2021b). Taken together, these cases suggest that predation by freshwater
459 macrocrustaceans remains insufficiently documented, particularly outside crayfish-based
460 systems and in habitats where direct observation is difficult (Waraniak et al. 2018), such as
461 subterranean, structurally complex, or low-visibility environments, which are also neglected
462 habitats despite harboring a considerable amount of threatened biodiversity (Bichuette and
463 Gallão 2021). Another barrier to understanding macrocrustacean–resource interactions is the
464 limited capacity of traditional gut content studies to accurately identify the food consumed,

since the finely grinded food impairs visual identification of the gut contents, unless expensive meta-barcoding techniques are employed.

Parasitic interactions between macrocrustaceans and freshwater fishes were comparatively underrepresented in our review, both in the number of studies and in the diversity of recorded interaction links. Despite the limited number of links, parasitic macrocrustaceans probably use a broader range of fish hosts than was represented in our dataset. Although interactions between parasitic macrocrustaceans and fish are less documented in the literature, other classes of parasitic crustaceans show a high diversity of interactions with freshwater fish, such as Copepoda (e.g. Luque et al. 2013) and Branchiura (Oliveira et al. 2017). The predominance of Cymothoidae reflects its well-known role as one of the most conspicuous and frequently studied groups of parasitic isopods, particularly due to their relatively large body size, visible attachment to hosts, and direct ecological impacts (Smit et al. 2014; Boxshall and Hayes 2019), being frequently reported in freshwater systems (Virgilio et al. 2020). Of the 45 valid genera of Cymothoidae, 10 are exclusively freshwater, 3 are both marine and freshwater and 30 are entirely marine (Boxshall and Hayes 2019). In contrast, other parasitic crustacean groups, such as Aegidae, appear to be comparatively less represented in the literature, despite their widespread occurrence (Suresh et al. 2022). This discrepancy likely reflects detection and research biases, as fish parasitism research in freshwaters also only included a few fish families (Smit et al. 2019). Furthermore, many parasitic interactions may be documented primarily in parasitological or aquaculture contexts, or recorded in unpublished fish monitoring data, rather than in studies explicitly addressing ecological interactions, which may have contributed to their underrepresentation in syntheses such as ours. That is, this apparent scarcity may have been further influenced by our choice of Boolean search terms and exclusion criteria, which were designed to capture ecological

interactions but may have overlooked studies where parasitism is reported without being framed within an interaction-based context, such as in taxonomic studies.

Finally, classifying studies according to the origin of the organisms provides an additional perspective on the role of biological invasions in the literature on fish-macrocrustacean interactions. Although most studies involved interactions between native organisms, the second most frequent category comprised native fishes interacting with non-native macrocrustaceans, mainly crayfish. This pattern reinforces the prominence of non-native crayfish in freshwater invasion research and reflects their capacity to affect native communities through predation, competition, habitat modification, and other ecological mechanisms (Reynolds 2011; Britton et al. 2023; O'Hea-Miller et al. 2024). Furthermore, the lower proportion of studies involving non-native species may indicate that biological invasions remain comparatively underrepresented in relation to interactions exclusively of native species, despite representing one of the main threats to biodiversity in freshwater environments (Sayer et al. 2025). Therefore, future studies are needed to investigate this knowledge gap regarding biological invasions, in the context of fish-macrocrustacean interactions, and how they contribute to structuring freshwater systems.

CONCLUSION

This study provides a comprehensive global synthesis of published information on fish-macrocrustacean interactions in freshwater environments, revealing strong biases in current knowledge. Despite the ecological importance and broad distribution of both groups, the available literature remains limited and strongly skewed toward trophic interactions, especially predation. Research effort was also unevenly distributed across geographic regions, habitats, and taxonomic families, with streams, lakes, and rivers receiving most attention, while wetlands and several family-level combinations remain poorly represented.

The recurrent prominence of crayfish further indicates that current knowledge is strongly shaped by a few well-established model systems, including those associated with biological invasions. Although most studies involved native fishes and native macrocrustaceans, interactions involving non-native macrocrustaceans emerged as an important component of the literature, highlighting the need to better understand how non-native organisms reshape fish-macrocrustaceans interaction networks.

Together, these findings highlight a pronounced Eltonian shortfall regarding fish-macrocrustacean interactions in freshwater ecosystems. Addressing these gaps will require expanding research across underrepresented habitats, interaction types, and taxonomic families. Establishing a more balanced and comprehensive understanding of species interactions is essential to improve predictions of community responses to environmental change and to support effective conservation strategies in freshwater systems.

DATA AVAILABILITY STATEMENT

The step-by-step analysis is available in R code, raw data, and the complete list of selected studies are available in a GitHub repository (https://github.com/JH-All/fish_crustaceans_interactions).

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SUPPLEMENTARY MATERIAL

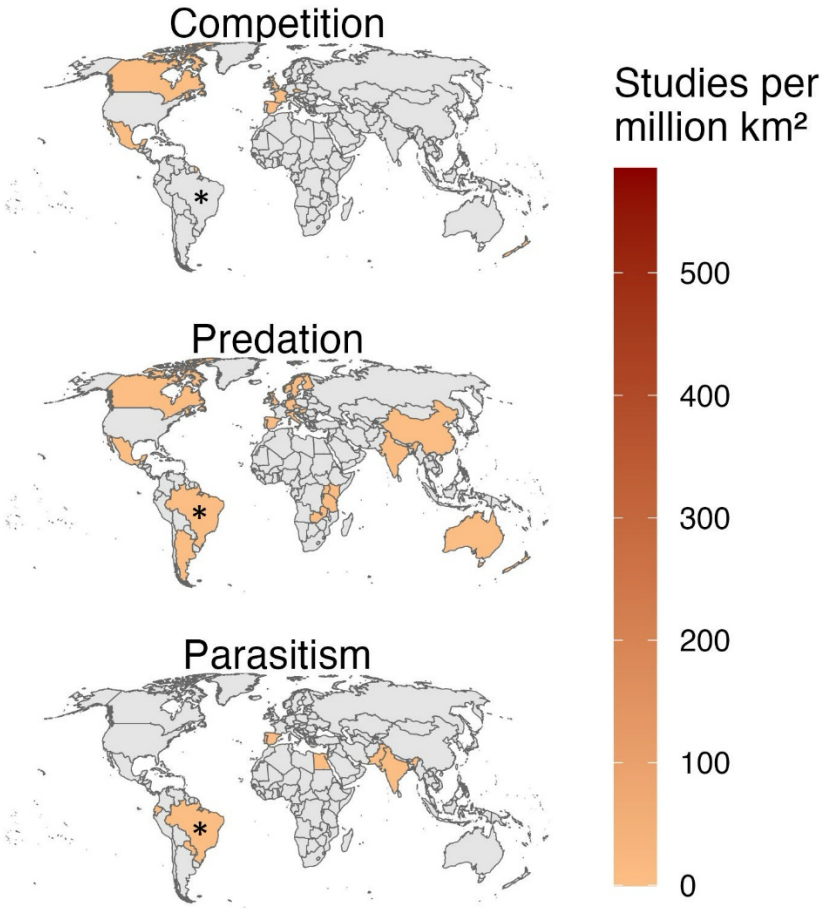

Figure S1. Global distribution of studies per million km^2 on macrocrustacean-fish interactions in freshwater environments by interaction type: competition, predation, and parasitism. Color intensity represents the number of studies per million km^2 per country. The asterisk in the maps indicates the only article dealing with commensalism involving fish and macrocrustaceans, registered for Brazil.

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772 **Table S1.** Summary of all articles addressing macrocrustacean-fish interactions in freshwater
773 environments considered in this study.

Article Title	Year of Publication
Invasive predatory fish occupies highest trophic position leading to expansion of isotopic niches in a riverine food web	2025
Evaluating brown trout as a potential biological control agent of signal crayfish	2025
Invasive swamp eels reduce aquatic animal diversity and disproportionately reduce prey for nesting wading birds	2025
Difficult to deal with: attempts for eradication of marbled crayfish from a small urban pond	2025
Identifying refugia from the synergistic threats of climate change and invasive species	2025
Hooked by the tongue: buccal parasitism of *Moenkhausia* spp. (Ostariophysi: Acestrorhamphidae) by *Paracymothoa astyanaxi* (Isopoda: Cymothoidae)	2025
Some Studies on Isopoda Infestation in Different Types of Cultured Fish with Special Reference to Treatment	2025
Community trophic structure within reservoirs changes in the presence of invasive Chinese mystery snail (*Cipangopaludina chinensis*) and northern crayfish (*Faxonius virilis*)	2025
Seasonal changes in trophic ecology of co-occurring freshwater invasive species at a thermal locality	2025
Identifying key drivers of extinction for Chitala populations: data-driven insights from an intraguild predation model using a Bayesian framework	2024
Ectoparasite crustaceans of ten fish species from the upper Araguari River in northern Brazil	2024
Description of the Life Cycle Stages of the Parasitic Cymothoid, *Cymothoa indica* Schioedte and Meinert, 1884, and Its Prevalence in Commercial Fishes from Chilika Lagoon, India	2024
Hydrology-mediated ecological function of a large wetland threatened by an invasive predator	2023
Testing whether reducing brown trout biomass in peatland lakes increases macro-invertebrate biomass and invertivorous waterbird occurrence	2023
Strong temporal variation of consumer δ13C value in an oligotrophic reservoir is related to water level fluctuation	2023
Predation of the Federally Endangered Roanoke Logperch (*Percina rex*) by the Invasive Ozark Crayfish (*Faxonius ozarkae*)	2022
New records and hosts of the isopod *Telotha henselii* (Isopoda: Cymothoidae) in Ecuadorian Amazonia	2022
Ecosystem effects of invasive crayfish increase with crayfish density	2022
Age-Structured Interactions among Reintroduced Sockeye Salmon, Resident Kokanee, Invasive Mysids, and their Zooplankton Prey in Skaha Lake, British Columbia	2021
Effect of multimodal cues from a predatory fish on refuge use and foraging on an amphidromous shrimp	2021
Habitat and host associations of the fish-burrowing parasite *Artystone minima* (Cymothoidae: Isopoda) in eastern Amazonia	2021
Effect of burrowing cymothoid parasitism on loricariids	2021

Nonconsumptive predator effects modify crayfish-induced bioturbation as mediated by limb loss: Field and mesocosm experiments	2020
New records of *Riggia cryptocularis* (Isopoda: Cymothoidae) parasitizing two *Odontostilbe* species (Characiformes: Characidae) in the Paraguay River Basin, Paraguay, with a review of Riggia host species	2020
Ontogenetic diet shifts with potential ramifications for resource competition in a kokanee–Mysis diluviana system	2020
Effects of River Hydrology and Physicochemistry on Anchovy Abundance and Cymothoid Isopod Parasitism	2019
First report of *Artystone trysibia* (Isopoda: Cymothoidae) in *Caquetaia spectabilis* (Cichliformes: Cichlidae)	2019
Behavioral interactions and trophic overlap between invasive signal crayfish *Pacifastacus leniusculus* (Decapoda, Astacidae) and native fishes in Iberian rivers	2019
La Niña' phenomenon and the relationship between decapod populations and fishes in temporarily isolated shallow lakes	2017
Effect of water quality parameters on isopod parasite *Aitropus typus* (Aegidae) of ectotherms in Chashma lake, Pakistan	2016
Macroparasites of allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*) of the Western Iberian Peninsula Rivers: ecological, phylogenetic and zoonotic insights	2015
Predation by signal crayfish *Pacifastacus leniusculus* on fish eggs and its consequences for coregonid recruitment	2015
Effects of flow on lateral interactions of fish and shrimps with off-channel habitats in a large river-floodplain system	2014
Salvelinus namaycush spawning substratum attracts egg predators and opportunists through chemosensory cues	2014
Predation on invasive redclaw crayfish *Cherax quadricarinatus* by native fishes in the Kafue River, Zambia	2014
Cleaning interactions between shrimps (Palaemonidae) and freshwater stingrays (Potamotrygonidae) in the Paraná River, Southeastern Brazil	2014
Invasive crayfish Orconectes Rusticus (Decapoda, Cambaridae) is a more effective predator of substrate nesting fish eggs than native crayfish (*O. Virilis*)	2013
Scavenger or predator? Examining a potential predator-prey relationship between crayfish and benthic fish in stream food webs	2013
Indirect effects of invasive crayfish on native fish parasites	2013
Invasive crayfish in a high desert river: Implications of concurrent invaders and climate change	2012
Opportunistic predation of fish by anomuran crabs (Crustacea, Anomura, Aeglidae) in rivers of southern Brazil	2012
An invasive crayfish affects egg survival and the potential recovery of an endangered population of Arctic charr	2011

Predation of lake trout and lake whitefish embryos by crayfish: Implications of shifts in crayfish dominance in Lake Simcoe	2011
Predation on a cave fish by the freshwater crab *Avotrichodactylus bidens* (Bott, 1969) (Brachyura, Trichodactylidae) in a Mexican sulfur cave	2011
Predation on early life stages of lake sturgeon in the Peshtigo river, Wisconsin	2010
Changes in abundance of Nile shrimp, *Caridina nilotica* (Roux) following the decline of Nile perch and recovery of native haplochromine fishes, Lake Victoria, Tanzanian waters	2010
Effects of a conservative rock bass length limit on angler participation, sport fish populations, and crayfish prey in a Missouri Ozark stream	2010
Biological control of invasive populations of crayfish: The European eel (*Anguilla anguilla*) as a predator of *Procambarus clarkii*	2010
Factors affecting sea lamprey egg survival	2009
Environmental factors influencing adult sex ratio in Trinidadian guppies	2009
Shifts between biotic and physical driving forces of species organization under natural disturbance regimes	2009
Spatial and temporal variation in the effects of fish and crayfish on benthic communities during stream drying	2009
Ornamental evolution in Trinidadian guppies (*Poecilia reticulata*): Insights from sensory processing-based analyses of entire colour patterns	2008
Behavioural laterality in the shrimp-eating cichlid fish *Neolamprologus fasciatus* in Lake Tanganyika	2008
Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish	2007
Abiotic factors, competition or predation: What determines the distribution of young crayfish in a watershed?	2007
Crayfish in lakes and streams: Individual and population responses to predation, productivity and substratum availability	2006
Predation by rainbow trout (*Oncorhynchus mykiss*) on a Western Australian icon: Marron (*Cherax cainii*)	2007
Influence of egg predation and physical disturbance on lake trout Salvelinus namaycush egg mortality and implications for life-history theory	2007
Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: A whole-lake experiment	2006
Effect of parasitism on plasma sex-specific proteins in *Cyphocarax gilbert* (Teleost, Curimatidae)	2005
Disentangling the selective factors that act on male colour in wild guppies	2006
Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools	2004
Nest defense against predators by the male fringed darter (*Etheostoma crossopterum*)	2004
Interactions of common carp (*Cyprinus carpio*) with benthic crayfish decapods in shallow ponds	2004
Resource-consumer relationships in Lake Victoria, East Africa	2003
Seasonal foraging by channel catfish on terrestrially burrowing crayfish in a floodplain-river ecosystem	2003
Tracking trophic interactions in coldwater reservoirs using naturally occurring stable isotopes	2002

No general percid dominance at mesotrophic lake conditions: Insights from the quantification of predator-prey interactions	2002
How host size may constrain the evolution of parasite body size and clutch size. The parasitic isopod *Ichthyoxenus fushanensis* and its host fish, *Varicorhinus bacbatulus*, as an example	2001
Neomysis integer in a shallow hypertrophic brackish lake: Distribution and predation by three-spined stickleback (*Gasterosteus aculeatus*)	2000
Habitat use by crayfish in stream pools: Influence of predators, depth and body size	2000
Distribution of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physico-chemistry, predatory fish, and invertebrate prey	2000
Grazer identity changes the spatial distribution of cascading trophic effects in stream pools	2000
Why selection favors protandrous sex change for the parasitic isopod, *Ichthyoxenus fushanensis* (Isopoda: Cymothoidae)	1999
Effects of fish on the local abundance of crayfish in stream pools	1999
Trophic interactions between yellow perch (Perca flavescens) and their benthic prey in a littoral zone community	1998
Gill parasites of mummichogs, *Fundulus heteroclitus* (Teleostei: Cyprinodontidae): Effects of season, locality, and host sex and size	1998
Ecological impact of introduced crayfish on benthic fishes in a British Lowland River	1997
The introduction of freshwater fish and crayfish species in the Camargue : History, origins and changes in assemblages	1997
The effects of size-dependent predation risk on the interaction between behavioral and life history traits in a stream-dwelling isopod	1996
Pike and red swamp crayfish: A new case on predator-prey relationship between aliens in central Spain	1996
Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*	1995
The roles of predation, competition, and exploitation in the trophic dynamics of a warmwater stream: a model synthesis, analysis, and application	1994
Using growth/mortality trade-offs to explore a crayfish species replacement in stream riffles and pools	1993
Species replacements among Orconectes crayfishes in Wisconsin lakes: the role of predation by fish	1993
Nile perch, Lates niloticus, predation on the freshwater prawn, *Caridina nilotica*, in the Nyanza Gulf, Lake Victoria, East Africa	1992
An experimental study of the effects of predatory fish on macroinvertebrates in a Hong Kong stream	1991
Crayfish control with traps and largemouth bass	1989
Nest defense and aggressive interactions between a small benthic fish (The Johnny Darter *Etheostoma nigrum*) and crayfish	1989
Habitat use and fish avoidance behaviors by the stream-dwelling isopod *Lirceus fontinalis*	1988
Interactions between an exotic crayfish and stocked rainbow trout in newcastle reservoir, Utah	1987
An analysis of the mechanisms governing species replacements in crayfish	1985
Role of the crayfish cherax destructor clark as food for trout in lake Eucumbene, New South Wales	1983

Effects of Brook Trout Predation on a Crayfish Population	1967
Active predation of crayfish on fishes	1961

774