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Systematic Review of Parasite Diversity in Wild Freshwater Fishes and Their Host-Locality Interactions in Türkiye

Canan Hamurkaroğlu¹  | Ahmet Özer²  | Nazan Danacıoğlu³  | Ayten Yiğiter⁴ 

¹Department of Actuarial Sciences, Faculty of Business Administration, Karabük University, Karabük, Turkey | ²Faculty of Fisheries and Aquatic Sciences, Diseases Division, Sinop University, Sinop, Turkey | ³Department of Data Science and Analytics, Faculty of Science and Letters, Sinop University, Sinop, Turkey | ⁴Department of Statistics, Faculty of Science, Hacettepe University, Ankara, Turkey

Correspondence: Ahmet Özer (aozer@sinop.edu.tr)

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ABSTRACT

This systematic review documented a taxonomically diverse parasite fauna of freshwater fishes across seven geographical regions of Türkiye, encompassing 11 phyla: Acanthocephala, Annelida, Arthropoda, Choanozoa, Ciliophora, Cnidaria, Euglenozoa, Mollusca, Myxozoa, Nematoda, and Platyhelminthes. UpSet charts were created to display and analyze intersections among multiple groups of freshwater localities, higher-level parasite and host fish taxa, and families. To visualize documented host–parasite relationships in the wild freshwater dataset, a bipartite network was constructed with freshwater fish and parasite families as nodes. Shannon diversity values calculated from documented parasite species assemblages were used in k-means clustering to identify host groups with different parasite diversity profiles. The most species-rich taxon was Platyhelminthes, accounting for 60.14% of all recorded parasite species, followed by Nematoda, the second-largest group, accounting for 10.14%; the other taxa contributed smaller proportions. At the class level, Monogenea accounted for the largest proportion, representing 34.06% of all identified parasite species in the overall diversity, followed by Trematoda (14.49%) and Cestoda (11.59%), all of which accounted for significant portions of the dataset. The Marmara region was the most species-rich freshwater environment in terms of both host fish and parasite diversity at the family level. Generalists, such as trematodes (Diplostomidae), cestodes (Bothriocephalidae), and copepods (Lernaeidae), and specialists, such as monogeneans (Dactylogyridae and Ancylostomidae), were illustrated using heatmaps and networks to reveal their host ranges across seven freshwater environments.

1 | Introduction

Parasites are a key part of biodiversity, influencing processes from individual organisms to entire communities. They also play a crucial role in ecosystem functioning, structure, and trophic dynamics, as well as in predicting the future of natural systems (Marcogliese and Cone 1997; Studer et al. 2010; Lafferty et al. 2006; Wood et al. 2007; Kuris et al. 2008). They also shape and regulate host population dynamics and contribute considerably to the energy flow within ecosystems (Franier et al. 2018;

Hudson et al. 1998; Lefèvre et al. 2009; Thielges et al. 2008). In addition to supporting these ecosystem processes, parasites also serve as indicators of hosts' biological aspects and environmental quality, owing to their complex life cycles and significant interactions within ecosystems (Lafferty 1997; Huspeni and Lafferty 2004; Marcogliese 2005; Vidal-Martínez et al. 2010; Shea 2012; Nachev and Sures 2016). Biological invasions pose major threats to ecosystems, and invasive species are among the largest threats to global biodiversity (Pimentel et al. 2001; Torchin et al. 2002). Invasive host species can impact ecosystem functions via the

Correction added on 29-July-2026, after first online publication: The copyright line was changed.

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parasites they carry (Chalkowski et al. 2018). In these invasions, parasites, whether specialist or generalist, are among the key factors shaping interactions among native, non-native, endemic, and cross-basin-introduced fishes (Torchin et al. 2003; Poulin and Mouillot 2003; Civitello et al. 2015). In ecological dynamics such as host–parasite relationships, the structure of parasite communities operates at two interconnected scales (Rynkiewicz et al. 2019). At the host scale, parasites are linked to individual hosts and exhibit complex adaptations that exploit host physiology, behaviour, and evolution (Poulin 2007; Preston et al. 2016). At the environmental scale, parasites and their communities function within the wider environment through interactions with multiple hosts and abiotic factors, such as climate, habitat, and nutrients, that influence their distribution (Sures 2004; Marcogliese 2016; Gordy et al. 2020). Therefore, understanding how animal communities assemble is a crucial goal for both current management practices and future predictive efforts (Brian and Aldridge 2022).

Fish parasites show extensive morphological and molecular diversity across both protozoan and metazoan groups. Most parasites found in fish belong to groups such as Ciliophora, Platyhelminthes (including Monogenea, Trematoda, and Cestoda), Cnidaria (Myxozoa), Nematoda, Arthropoda (Copepoda, Isopoda), Annelida, Mollusca, Acanthocephala, and several minor taxa. Some of these have been reported to significantly affect wild and cultured fish populations, as documented in global parasitological surveys (Salgado-Maldonado 2006; Shinn et al. 2015; Truong et al. 2022). Protozoan and metazoan parasites can have either direct or indirect life cycles. Some parasites, including ciliophorans, arthropods, hirudineans (leeches), and monogeneans, follow a direct cycle with fish as the mandatory host. Conversely, metazoan parasites such as myxozoans, acanthocephalans, cestodes, digeneans, and nematodes have indirect life cycles that involve at least two hosts, with fish serving as paratenic or intermediate hosts (Huston et al. 2020). Given the significance of fish in parasite life cycles, food webs, and ecosystem energy flow, it is crucial to characterize host–parasite diversity and community interactions at the national level. This helps elucidate the interactions among geographic regions, parasites, and hosts, as highlighted by recent studies.

Freshwater plays a crucial role in global biodiversity and human well-being, but freshwater biodiversity is in crisis worldwide due to escalating pressures and threats to ecosystems (Darwall et al. 2018). Overall, growing evidence indicates that freshwater ecosystems are undergoing rapid and significant changes driven by climate change and human-induced stressors. Türkiye has diverse water resources, including 25 river basins, most of which originate within the country and flow to the sea, with a few transboundary; 320 natural lakes of varying sizes; and 861 operational dams (SHW 2022), resulting in a highly diverse freshwater fish fauna comprising 431 fish species (Froese and Pauly 2026). In Türkiye, research on freshwater fish parasites, which began in 1964, has increased, particularly since the mid-1990s, peaking in 2011 and thereafter with fluctuations that parallel global trends; a total of 148 fish species have been reported as hosts of these parasites (Özer 2021, 2025). Thus, elucidating the interactions between fish hosts and their parasites at the whole countrywide scale is crucial for understanding their current status and predicting future trajectories amid the increasing impacts of the aforementioned factors.

In the present study, we conducted a bibliometric analysis of scientific studies on freshwater fish parasites published in journals, books, conference proceedings, and databases in Türkiye. More specifically, this analysis aimed to (i) investigate the temporal distribution of publications; (ii) investigate the research outputs from these publications on the parasite fauna of wild freshwater fish hosts at the family level; (iii) analyze the representations and interactions between fish hosts and parasites through data, network and cluster analysis; (iv) analyze the host–parasite community structures in seven geographical regions in Türkiye. These findings will, for the first time in Türkiye, reveal current parasite diversity in wild freshwater fishes and their interactions at the country level, identify knowledge gaps that may inform future research, and guide policymakers on future research directions in Türkiye.

2 | Materials and Methods

2.1 | Search Strategy and Data Collection

In this study, all relevant papers were obtained from online sources of the animal science databases (<https://www.cabidigitallibrary.org>, PubMed, Scopus, Web of Science, Google Scholar, Zoological Record, Biological Abstracts, Fisheries Abstracts, the research repository of Aquadocs) using the keywords: “parasite”, “fish”, “Türkiye” and “Turkey”, as well as published scientific articles, symposium proceedings, checklists and books, such as Özer (2021, 2025), which include the most up to date and comprehensive checklists on all wild freshwater fish parasites reported since 1964. A total of 350 scientific publications reported 276 parasite species across 165 freshwater fish host species in Türkiye. Genus-level-identified parasites from fish were also identified and included in the study if they were the sole report among all parasites. The scientific names of existing parasites were carefully checked and corrected using reliable sources, including the World Register of Marine Species (WoRMS; <http://www.marinespecies.org/index.php>; 2025). The scientific names of fish hosts were verified using the FishBase database (<https://www.fishbase.in/search.php>; 2025). When outdated names or synonyms were encountered in the literature, they were replaced with their currently accepted taxonomic names. Freshwater parasites reported from wild fish hosts were grouped by geographic origin into 7 regions: the Black Sea region, the Marmara Region, the Aegean region, the Mediterranean Region, the Central Anatolia region, the Eastern Anatolia region, and the Southeastern Anatolia region in Türkiye (Figure 1). Descriptive summary tables and some basic graphical representations of the freshwater datasets were generated using Microsoft Excel 365 (Microsoft Corporation 2023). All advanced data analyses and visualizations were conducted using the R statistical environment (R Core Team 2023). Data manipulation, filtering, and restructuring were performed using the *dplyr* package (Wickham et al. 2023), while data reshaping and preparation of tidy data formats were carried out using *tidyr* (Wickham and Girlich 2023). Structured data frames were managed using the *tibble* package (Müller and Wickham 2023).

General graphical visualizations, including bar charts and heatmap-based representations, were produced using *ggplot2* (Wickham 2016), with graphical layout and alignment

Türkiye: Geographical Regions and Seas

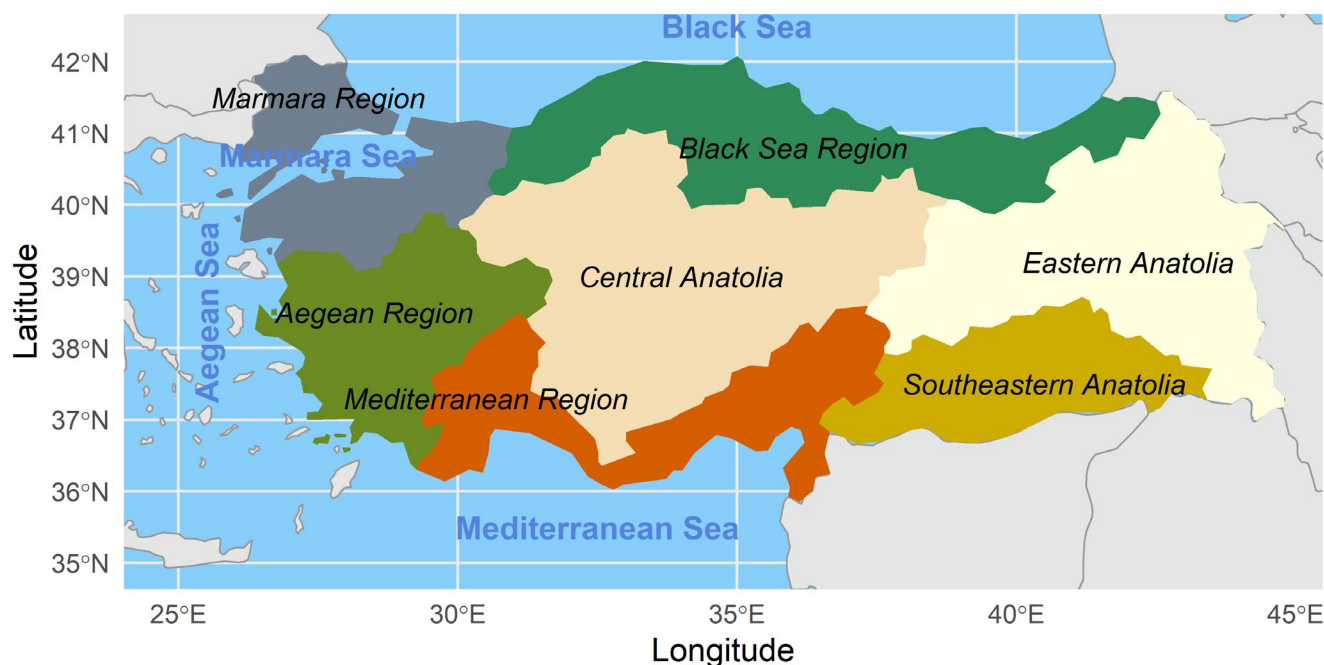


FIGURE 1 | Map illustrating the seven coloured geographical regions in Türkiye.

supported by the grid package (R Core Team 2023). UpSet plots, used to visualize complex intersections among parasite and host fish taxa across multiple marine localities, were generated using the *ComplexUpset* package (Krassowski 2023), which extends the *ggplot2* framework for scalable intersection analysis.

Network analyses representing host–parasite associations were conducted using the *igraph* package for graph construction and network metric calculation (Csardi and Nepusz 2006). Network data were subsequently transformed into *tidygraph* objects and visualized using *ggraph*, which applies the grammar of graphics paradigm to relational and network-based data (Pedersen 2020a, 2020b). K-means method was used for cluster analysis (Hartigan and Wong 1979).

This integrated software and package workflow ensured methodological consistency and reproducibility across all graphical and analytical outputs presented in the study.

2.2 | UpSet Charts and Heatmaps

UpSet plots were used to illustrate the intersections among freshwater localities, parasite taxa, and host fish taxa. Vertical bars represent intersection sizes, horizontal bars indicate total set sizes, and the dot matrix shows which sets are involved in each intersection (Lex et al. 2014). The heatmaps created in the present study were based on presence–absence data derived from documented occurrences of parasite and host fish families across geographical regions. Each region was considered separately, and the intersections represent families shared among regions.

2.3 | Network Analysis

Host–parasite interaction networks were constructed for wild freshwater fishes in Türkiye. Documented associations between fish families and parasite families were modelled using bipartite weighted networks (Dormann et al. 2009; Barrat et al. 2004). Fish and parasite families were represented as separate node sets, and their associations were represented as weighted edges. Edge weights reflected how frequently a particular fish family–parasite family association was reported in the literature and were visualized as proportional edge thickness. As these weights were based on published records, they indicate reporting frequency rather than the strength of biological interactions and may partly reflect differences in sampling effort and research attention among host and parasite groups. Family-level analyses were used to summarize broad patterns of documented host–parasite associations across regions using a consistent taxonomic framework. To improve the readability of the overall network visualization, an additional reduced network containing the 100 most frequently reported fish family–parasite family associations was generated. Standard network descriptors, including mean degree, weighted degree strength, connectance, modularity, and nestedness (NODF), were calculated to characterize the structure of the overall and regional networks (Dormann et al. 2009; Almeida-Neto et al. 2008).

2.4 | Cluster Analysis

To examine variation in documented parasite diversity among freshwater fish families, Shannon diversity indices (H') were calculated for parasite assemblage records reported from each fish family (Shannon 1948; Magurran 2004). The calculations were based exclusively on documented parasite species

reported in the literature. The Shannon index reflects both species richness and the distribution of species within an assemblage, with higher values indicating greater diversity. Shannon diversity values were subsequently used in k-means clustering to identify four groups characterized by different levels of documented parasite richness and dominance. A bipartite network was then constructed to visualize the associations between the identified clusters and fish families. In this network, edge thickness represented the Shannon diversity value associated with each record.

2.5 | Correlation Analysis

To assess whether differences in documented parasite diversity could partly reflect variation in research effort, correlations were calculated between host family reporting frequency (the number of documented records for each fish family) and parasite family richness (the number of parasite families reported from each fish family). Both Pearson's correlation coefficient and Spearman's rank correlation coefficient were used to evaluate the strength and direction of these relationships.

3 | Results

3.1 | Data Analysis

From the first publication in 1964 to the late 1980s, the number of publications remained consistently low (Figure 2). A modest increase became apparent in the early 1990s, though year-to-year fluctuations persisted. From the late 1990s onward, a more pronounced upward trend emerged, marked by a gradual increase in publication output. This increase became particularly evident after the early 2000s, reaching several local maxima between 2005 and 2010. The highest publication count was recorded in 2011 ($n=26$), followed by a sharp decline in subsequent years. After 2015, the annual number of publications showed marked variability, with intermittent increases and decreases, but

overall remained higher than levels observed prior to the 2000s. In parallel with these publications, the number of parasites reported per year from their wild freshwater fish hosts followed a similar pattern (Figure 3).

The Wild Freshwater dataset, including the scientific names of parasite and host taxa, the taxa to which they belong, geographical localities, publication year, and references from previously published studies, showcases parasite diversity across 11 higher taxa, including 17 classes, 70 families, and 276 species. The host diversity comprises 24 fish families and 148 species, spread across seven geographical regions. Figure 4 illustrates the number of parasites in these 11 higher taxa: Acanthocephala, Annelida, Arthropoda, Choanozoa, Ciliophora, Cnidaria, Euglenozoa, Mollusca, Myxozoa, Nematoda, and Platyhelminthes. The most species-rich taxon is Platyhelminthes, representing 60.14% ($n=166$) of all parasite species recorded. Nematoda is the second-largest group, accounting for 10.14% ($n=28$). Other groups contribute smaller shares: Ciliophora (7.25%; $n=20$), Cnidaria (5.07%; $n=14$), and Acanthocephala (4.71%; $n=13$). The remaining minor groups account for a small share of overall diversity. Overall, most recorded parasite species belonged to Platyhelminthes and Nematoda, which together accounted for more than 70% of all parasite species documented in the dataset.

The distribution of parasite species across major taxonomic classes was illustrated in Figure 5. Monogenea accounts for 34.06% ($n=94$) of all identified species, underscoring its key role in overall diversity. Next are Trematoda (14.49%, $n=40$), Cestoda (11.59%, $n=32$), and Enoplea (9.06%, $n=25$), which collectively account for a significant portion of the data. Oligohymenophorea (6.16%, $n=17$), Myxozoa (5.07%, $n=14$), and Copepoda (4.71%, $n=13$) have moderate contributions, while the remaining groups are represented by fewer species. The distribution of parasites in seven regions of Türkiye is shown at the phylum, class, family, and species levels in Figure 6A–D. Figure 6 presents the coverage of phylum-level ($n=11$), class-level ($n=17$), family-level ($n=70$), and species-level ($n=276$) distributions across these regions. At the

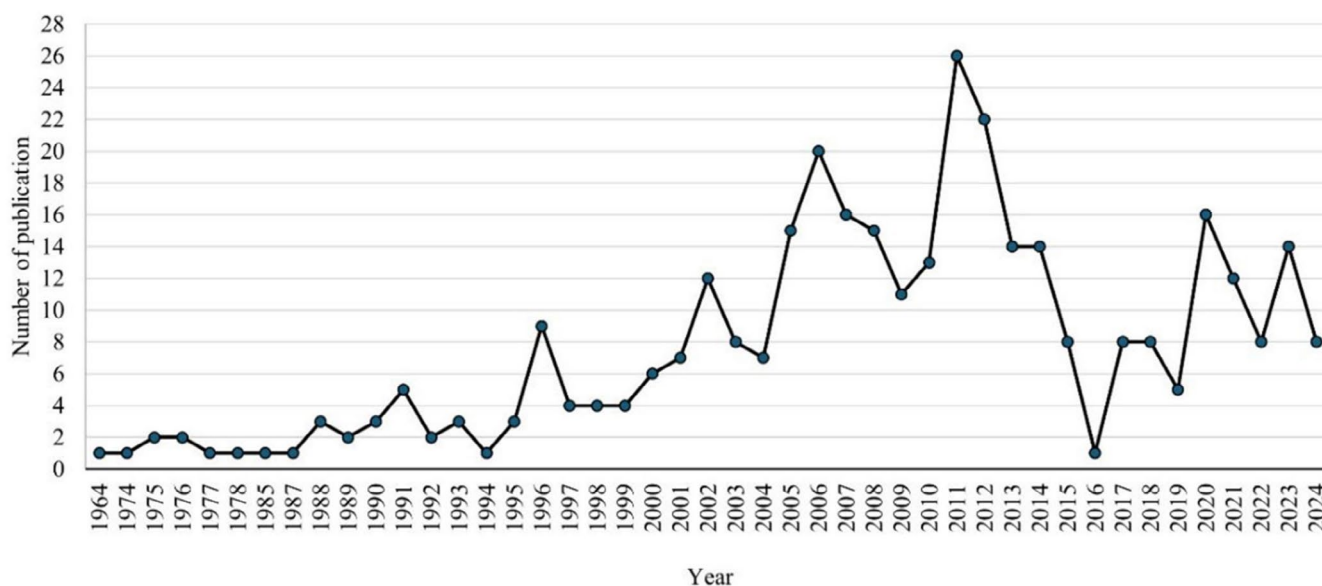


FIGURE 2 | Number of publications on wild freshwater fish parasites by year in Türkiye.

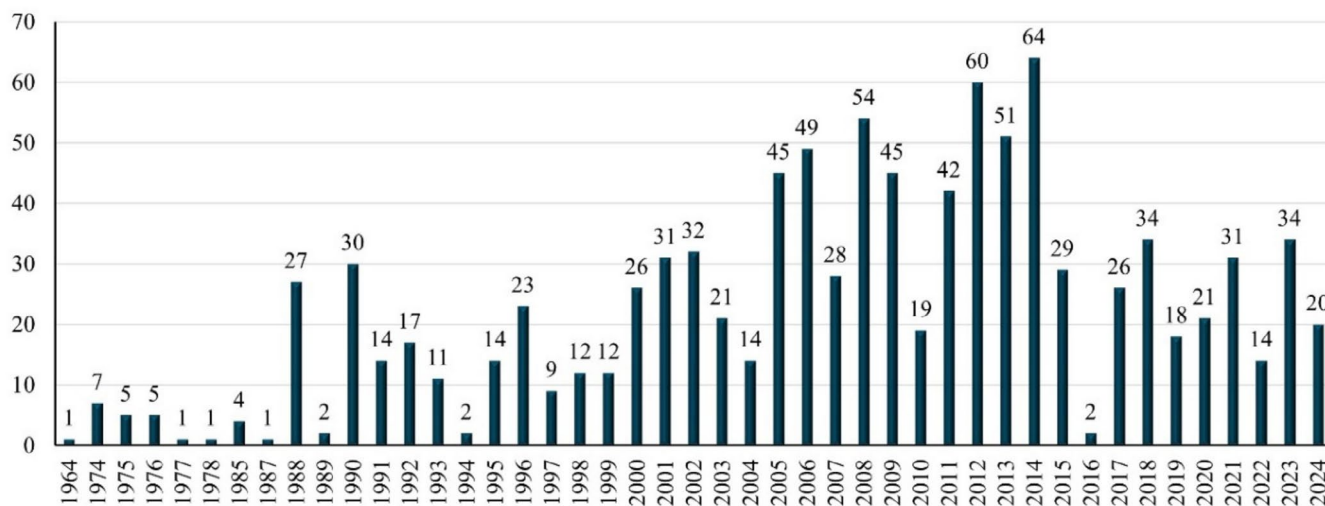


FIGURE 3 | Number of reported parasite species on wild freshwater fish hosts in publications by year in Türkiye.

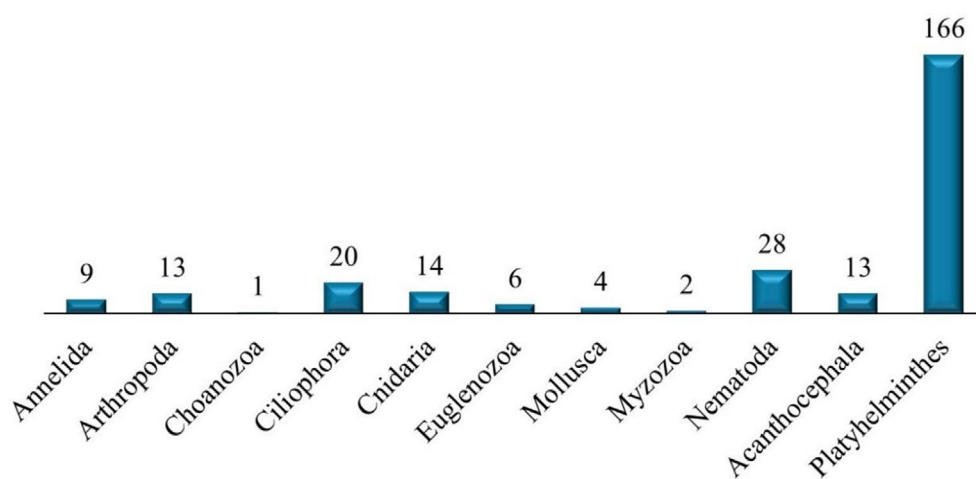


FIGURE 4 | Number of reported parasite species in publications on wild freshwater fish parasites by higher taxa in Türkiye.

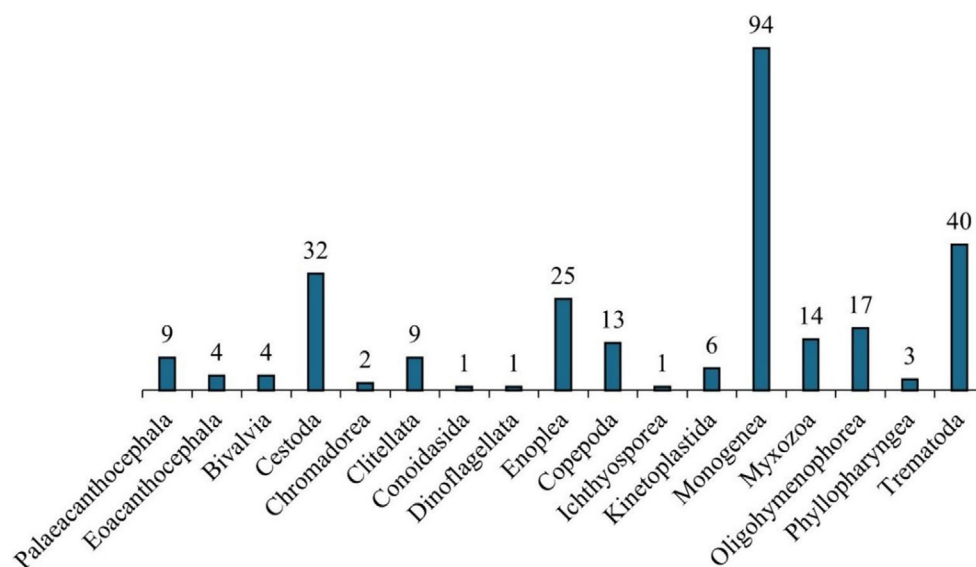


FIGURE 5 | Number of reported parasite species in publications on wild freshwater fish parasites at the class level in Türkiye.

phylum level, the Aegean, Central Anatolia, Eastern Anatolia, and Marmara regions displayed the highest taxonomic coverage, representing 81.82% ($n=9$) of the total higher taxon pool (Figure 6A). Among these, the Aegean and Marmara regions had the highest class-level coverage, at 76.47% (13 classes) (Figure 6B). The Marmara region exhibited the highest

parasite diversity at the family level (64.79%; $n=46$) and at the species level (46.38%; $n=128$) among the seven regions (Figure 6C,D). Regarding host fish diversity at the family level, the Marmara region had the highest value (66.67%, $n=16$), whereas at the species level, the Mediterranean region had the highest host diversity (30.32%, $n=47$) (Figure 7). This figure

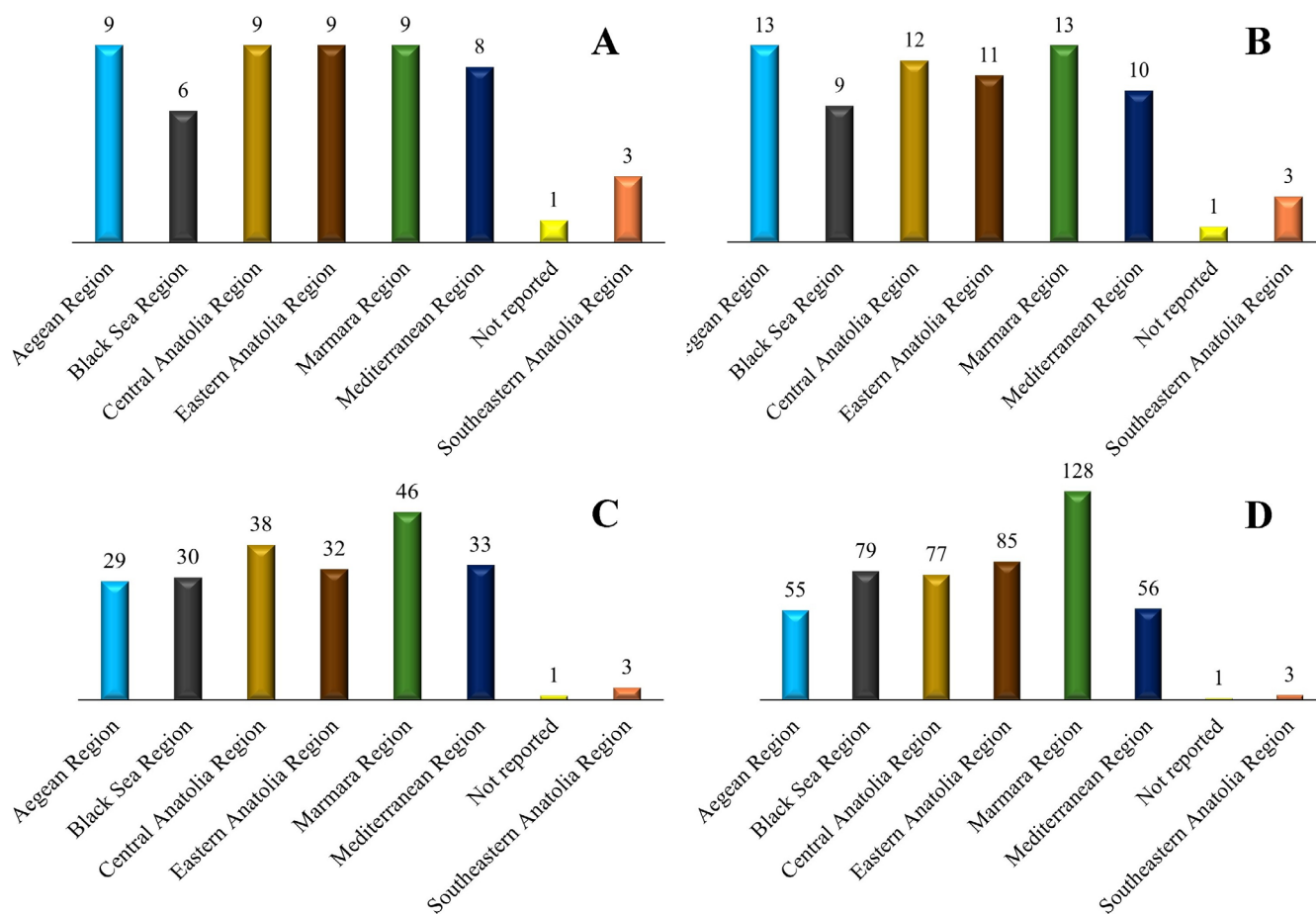


FIGURE 6 | Number of reported parasite taxa in publications on wild freshwater fish across the seven geographical regions in Türkiye, (A) Phylum level, (B) Class level, (C) Family level, (D) Species level.

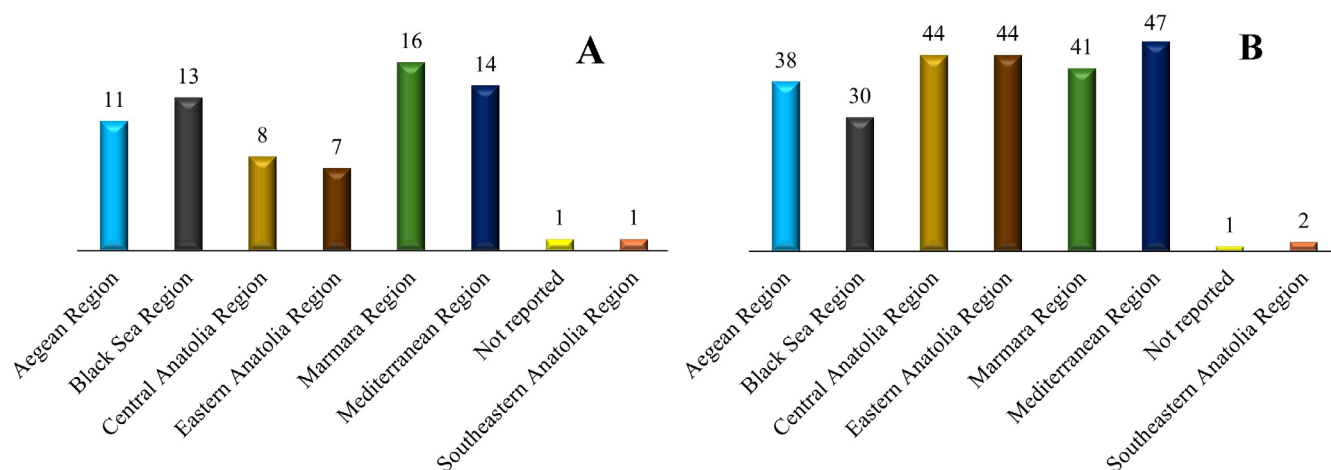


FIGURE 7 | Number of reported host fish taxa in publications on wild freshwater fish parasites across the seven geographical regions in Türkiye, (A) Family level, (B) Species level.

also displays host diversity at both the family and species levels in the other regions. The intersections among multiple parasite families across seven geographical regions illustrate that the Marmara region has the highest parasite family richness, including combinations ($n = 46$), followed by Central Anatolia ($n = 38$), the Mediterranean ($n = 33$), Eastern Anatolia ($n = 32$), the Black Sea ($n = 30$), and the Aegean ($n = 28$) (Figure 8). No reports were recorded from the South-Eastern Anatolia region. Moreover, 12 parasite families (17.1%) were reported from six geographical regions, representing the most frequently shared distribution pattern observed in the dataset (Table 1). The highest proportion reported in a single region is in the Marmara region ($n = 7$; 10.0%), followed by Central Anatolia ($n = 6$; 8.6%), the Black Sea ($n = 5$; 7.1%), and Eastern Anatolia ($n = 4$; 5.7%). Other regions exhibit lower diversity in combination patterns (see Table 1 for details). Although several parasite families were reported from multiple geographical regions, others were reported only from particular regions, indicating variation in the documented parasite family composition across Türkiye (Table 1). When the intersections among multiple families of fish hosts in seven geographical regions are considered, the highest host fish family richness is observed in the Marmara region ($n = 16$), followed by the Mediterranean region ($n = 14$), the Black Sea ($n = 13$), the Aegean region ($n = 11$), the Central Anatolia region ($n = 8$), and the Eastern Anatolia region ($n = 7$) (Figure 9). The largest distribution patterns included two fish families (8.3%). This occurred in three cases: two families were reported only from the Mediterranean region, two were shared between the Marmara and Aegean regions, and two families (Cyprinidae and Leuciscidae) were reported from six geographical regions (Table 2).

The heatmap revealed a sparse pattern, with many fish family-parasite family combinations absent from the dataset (Figure 10). Despite this, some associations appeared repeatedly across the matrix. In particular, Cyprinidae and Leuciscidae were associated with more reported parasite families than most other fish families. In contrast, many host families were associated with only a few documented parasite families. Among parasites, families such as Diplostomidae, Diphylobothriidae, Bothriocephalidae, Ergasilidae, and Lernaeidae were reported from multiple host groups and showed recurring patterns in the heatmap. Because these results are based on published records, the observed patterns may reflect differences in host diversity, reporting intensity, and research effort, as well as underlying biological relationships.

When geographical regions were examined separately, the Aegean region contained records of 28 parasite families associated with 11 wild freshwater fish families. In the corresponding heatmap (Figure S1A), fish families such as Leuciscidae and Cyprinidae were associated with a relatively large number of reported parasite families. In contrast, many other fish families were linked to only one or a few parasite families in the available records. Among parasite families, Dactylogyridae, Gyrodactylidae, Argulidae, Diplostomidae, Caryophyllidae, and Pomphorhynchidae were reported from more than one host fish family, whereas others were recorded from fewer host families. In the Black Sea region (Figure S1B), 30 parasite families were reported from 13 wild freshwater fish families. Leuciscidae, Cyprinidae, and Aphaniidae were associated with more reported parasite families than most other host families in this region. Several parasite families, including Trichodinidae, Diplostomidae, and Bothriocephalidae, were reported from multiple host fish families, whereas others were recorded from

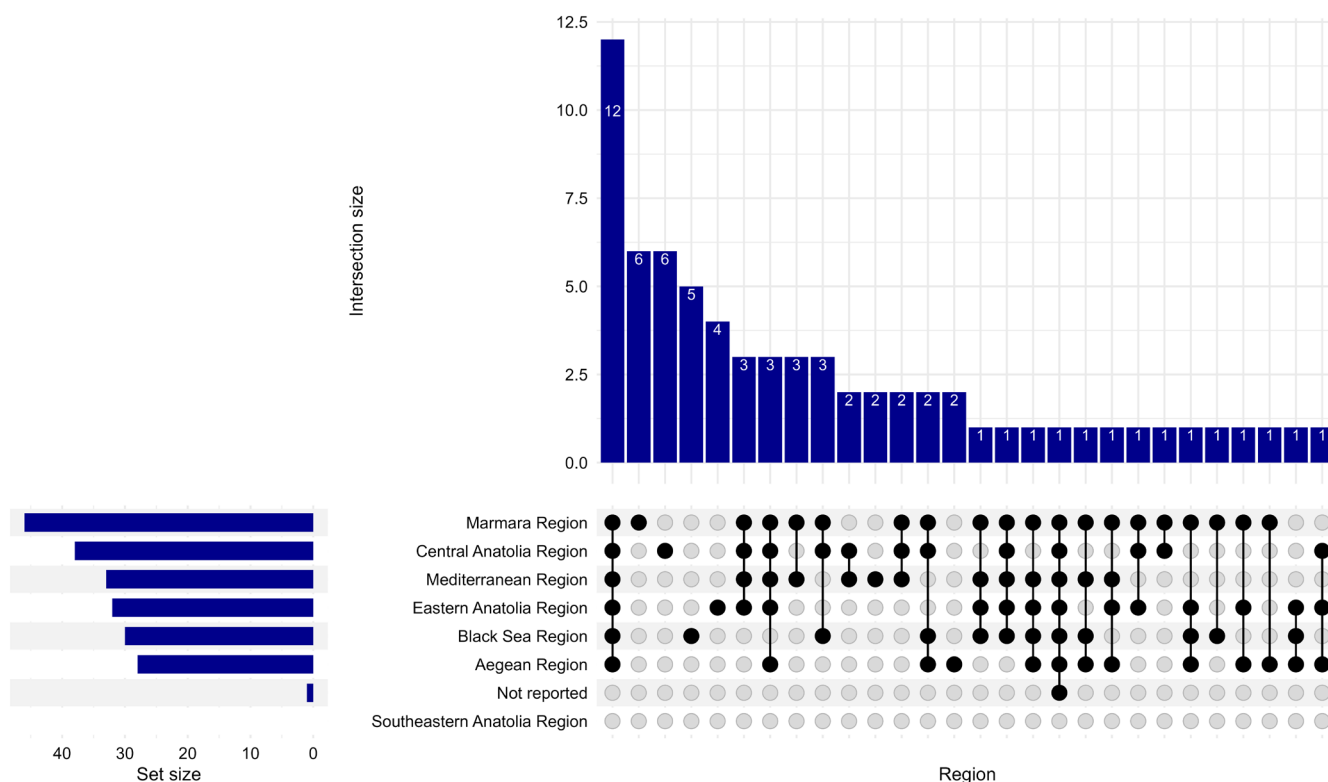


FIGURE 8 | Intersections among multiple parasite families across seven geographical regions in Türkiye.

TABLE 1 | Combination of parasite families by geographical regions in Türkiye.

Pattern	Region	Family (n)	Parasite families	%
11111100	MR + MEDR + BSR + AR + CAR + EAR	12	Allocreadiidae, Anisakidae, Argulidae, Bothriocephalidae, Caryophyllaeidae, Dactylogyridae, Diplostomidae, Diplozoidae, Eoechinorhynchidae, Gyrodactylidae, Lernaeidae, Trichodinidae	17.1
10000000	MR	7	Acuariidae, Aspidogastridae, Diplodiscidae, Opisthorchiidae, Pseudodactylogyridae, Quimperiidae, Trianophoridae	10
00001000	CAR	6	Aporocotylidae, Cryptobiaceae, Digenea, Gryporhynchidae, Hirudinidae, Sphaerosporidae	8.6
00100000	BSR	5	Echinochasmidae, Echinostomatidae, Gnathostomatidae, Heterophidae, Scyphidiidae	7.1
00000100	EAR	4	Diclybothriidae, Lernaeopodidae, Lytocestidae, Piscinoodinium	5.7
00010000	AR	3	Opecoelidae, Triaenophoridae, Ichthyosporea incerta sedis	4.3
10101000	MR + BSR + CAR	3	Capillariidae, Clinostomidae, Epistylididae	4.3
11000000	MR + MEDR	3	Anguillacolidae, Bucephalidae, Orientocreadiidae	4.3
11001100	MR + MEDR + CAR + EAR	3	Piscicolidae, Proteocephalidae, Rhabdochonidae	4.3
11011100	MR + MEDR + AR + CAR + EAR	3	Glossiphoniidae, Ichthyophthiriidae, Pomphorhynchidae	4.3
01000000	MEDR	2	Gorgoderidae, Quadrigyridae	2.9
01001000	MEDR + CAR	2	Eimeriidae, Trypanosomatidae	2.9
10111000	MR + BSR + AR + CAR	2	Chilodonellidae, Raphidascarididae	2.9
11001000	MR + MEDR + CAR	2	Lissorchiidae, Tetraonchoididae	2.9
00011100	AR + CAR + EAR	1	Philometridae	1.4
00110100	BSR + AR + EAR	1	Camallanidae	1.4
10001000	MR + CAR	1	Bodonidae	1.4
10001100	MR + CAR + EAR	1	Skrjabillanidae	1.4
10010100	MR + AR + EAR	1	Unionidae	1.4
10100000	MR + BSR	1	Strigeidae	1.4
10110100	MR + BSR + AR + EAR	1	Myxobolidae	1.4
11010100	MR + MEDR + AR + EAR	1	Echinorhynchidae	1.4
11100100	MR + MEDR + BSR + EAR	1	Ancylo-discoididae	1.4
11101100	MR + MEDR + BSR + CAR + EAR	1	Ancyrocephalidae	1.4
11110000	MR + MEDR + BSR + AR	1	Diectophymidae	1.4
11110100	MR + MEDR + BSR + AR + EAR	1	Ergasilidae	1.4
11111101	MR + MEDR + BSR + AR + CAR + EAR + NR	1	Diphyllbothriidae	1.4

Abbreviations: AR, Aegean Region; BSR, Black Sea Region; CAR, Central Anatolia Region; EAR, Eastern Anatolia Region; MEDR, Mediterranean Region; MR, Marmara Region; SAR, Southern Anatolia Region.

fewer host families. Overall, the heatmap revealed substantial variation in the distribution of documented host–parasite associations among fish families in the Black Sea region. In the Central Anatolia region (Figure S1C), associations were recorded among 38 parasite families and 8 wild freshwater fish families. Reported associations were concentrated in a limited number of host families, particularly Cyprinidae and Leuciscidae, which were linked to a relatively large number of parasite families in the available records, as reflected by the broader horizontal distribution of blue cells in the heatmap.

Finally, in the Mediterranean region (Figure S1F), 33 parasite families were reported from 14 wild freshwater fish families. Reported associations were concentrated among a limited number of host families, particularly Cyprinidae and Leuciscidae, which were linked to relatively many parasite families in the available records. As in the other regions, some parasite families were reported from multiple host families, whereas others were associated with fewer host families, indicating variation in the distribution of documented host–parasite associations among host groups.

To facilitate visualization of the overall network structure, a reduced network containing the 100 most frequently reported fish family–parasite family associations was examined (Figure 11; Table 3). On average, each node was connected to 3.7 other nodes, while the mean weighted degree strength was 60.67, reflecting the high reporting frequency of the retained associations. Cyprinidae and Leuciscidae were associated with the largest number of documented parasite family records in the reduced network. Among parasite families, Dactylogyridae, Diplostomidae, and Diphylobothriidae were associated with multiple host groups and were among the most frequently reported associations. The connectance value (0.211) indicated that approximately one-fifth of all possible fish family–parasite family associations were represented in the reduced network. The network also showed moderate nestedness ($\text{NODF} = 46.48$) and low modularity (0.219), suggesting that parasite families reported from less-connected host groups were often also recorded from host families with more documented associations.

TABLE 2 | Combination of fish families by geographical regions in Türkiye.

Pattern	Region	Family (n)	Fish families	%
01000000	MEDR	2	Cichlidae, Clariidae	8.3
10010000	MR + AR	2	Acheilognathidae, Centrarchidae	8.3
11111100	MR + MEDR + BSR + AR + CAR + EAR	2	Cyprinidae, Leuciscidae	8.3
00000100	EAR	1	Mastacembelidae	4.2
00100000	BSR	1	Syngnathidae	4.2
00110000	BSR + AR	1	Gasterosteidae	4.2
01011000	MEDR + AR + CAR	1	Gobionidae	4.2
01100000	MEDR + BSR	1	Poeciliidae	4.2
01110000	MEDR + BSR + AR	1	Aphaniidae	4.2
10000000	MR	1	Alosidae	4.2
10010100	MR + AR + EAR	1	Nemacheilidae	4.2
10100100	MR + BSR + EAR	1	Salmonidae	4.2
10101100	MR + BSR + CAR + EAR	1	Siluridae	4.2
10111000	MR + BSR + AR + CAR	1	Cobitidae	4.2
11000000	MR + MEDR	1	Anguillidae	4.2
11001001	MR + MEDR + CAR + NR	1	Tincidae	4.2
11011000	MR + MEDR + AR + CAR	1	Esocidae	4.2
11100000	MR + MEDR + BSR	1	Gobiidae	4.2
11100100	MR + MEDR + BSR + EAR	1	Mugilidae	4.2
11101000	MR + MEDR + BSR + CAR	1	Atherinidae	4.2
11110000	MR + MEDR + BSR + AR	1	Percidae	4.2

Abbreviations: AR, Aegean Region; BSR, Black Sea Region; CAR, Central Anatolia Region; EAR, Eastern Anatolia Region; MEDR, Mediterranean Region; MR, Marmara Region; SAR, Southern Anatolia Region.

(Table 3). Because the network was based on published records, these patterns should be interpreted as documented associations and may partly reflect differences in research effort among host groups.

The structures of the wild freshwater fish-parasite family networks were also determined for each of the seven geographical regions in Türkiye (Figure S2A–G). In the Aegean region, documented associations were concentrated in a relatively small number of fish families (Figure S2A). Among these, Leuciscidae was linked to more reported parasite families than most other host groups in the network. Frequently reported associations involved parasite families such as Diplostomidae, Dactylogyridae, Gyrodactylidae, Caryophyllaeidae, Allocreadiidae, and Bothriocephalidae. Cyprinidae was also associated with several parasite families and represented another important host group within the regional network. These patterns reflect the host–parasite family associations documented in the available literature for the Aegean region.

Within the Black Sea network (Figure S2B), Leuciscidae, Cyprinidae, and Aphaniidae were associated with more reported parasite families than most other host groups. Among parasites, Dactylogyridae, Trichodinidae, Diplostomidae, and

Gyrodactylidae appeared most frequently and were recorded from several host families. In contrast, many other parasite families were reported only occasionally and were linked to a limited number of host groups. Taken together, these records suggest that a relatively small number of host and parasite families account for a large proportion of the documented associations in the Black Sea region. A large proportion of the documented host–parasite family associations in Central Anatolia (Figure S2C) involved Cyprinidae and Leuciscidae, which were associated with more reported parasite families than most other host groups in the network. Cyprinidae was linked to a wide range of documented parasite families, including Gyrodactylidae, Dactylogyridae, Diplostomidae, Caryophyllaeidae, Rhabdochonidae, and Lernaeidae. Leuciscidae also showed numerous reported associations, particularly with parasite families such as Raphidascarididae, Lissoclinidae, Apatemonidae, and Diphyllbothriidae. Together, these two fish families accounted for a large proportion of the documented host–parasite family associations recorded for the Central Anatolia region. Cyprinidae accounted for many of the documented host–parasite family associations observed in the Eastern Anatolia network (Figure S2D). Frequently documented associations involved parasite families such as Dactylogyridae, Gyrodactylidae, Bothriocephalidae, Diplostomidae, and Caryophyllaeidae.



FIGURE 10 | Overall reported associations between wild freshwater fish and parasite families in six geographical regions.

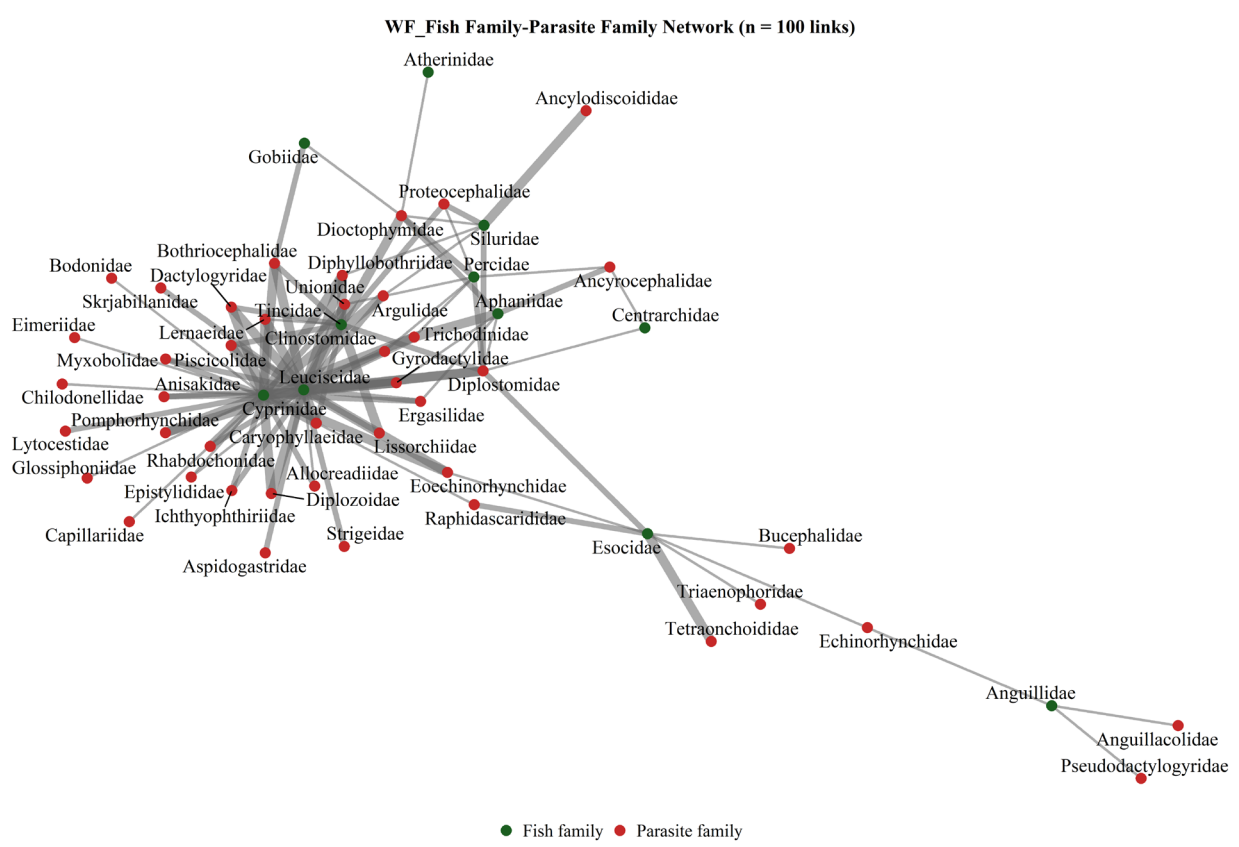


FIGURE 11 | Structure of the top 100 links of the Wild Freshwater fish-parasite family network in seven geographical regions in Türkiye.

TABLE 3 | Structural properties of the overall and regional wild freshwater fish–parasite family networks based on documented host–parasite associations in Türkiye.

Network	Nodes	Fish families	Parasite families	Edges	Total reporting freq.	Mean degree	Weighted degree strength	Connectance	Modularity	NODF	Links per species
Overall	93	24	69	273	1887	5.871	40.581	0.165	0.221	50.360	2.936
Overall top100	54	11	43	100	1638	3.704	60.667	0.211	0.219	46.477	1.852
Aegean	39	11	28	49	158	2.513	8.103	0.159	0.278	32.109	1.256
Black	43	13	30	73	239	3.395	11.116	0.187	0.275	52.558	1.698
Central Anatolia	46	8	38	88	236	3.826	10.261	0.289	0.255	61.084	1.913
Eastern Anatolia	39	7	32	68	325	3.487	16.667	0.304	0.140	54.794	1.744
Marmara	62	16	46	139	719	4.484	23.194	0.189	0.258	47.108	2.242
Mediterranean	47	14	33	67	205	2.851	8.723	0.145	0.380	35.038	1.426
Southeastern Anatolia	4	1	3	3	4	1.5	2	1	0		0.75

Leuciscidae, Mugilidae, and Siluridae were also linked to several parasite families and contributed substantially to the documented host–parasite associations in the region. The network included parasite families representing major taxonomic groups, including digeneans, monogeneans, cestodes, and nematodes. In contrast, some parasite families, such as Anisakidae, Philometridae, and Proteocephalidae, were recorded from fewer host groups and represented by fewer documented associations. Among the fish families represented in the Marmara network (Figure S2E), Cyprinidae and Leuciscidae were associated with more reported parasite families than most other host groups. Frequently documented associations involved parasite families such as Diplostomidae, Dactylogyridae, Gyrodactylidae, and Bothriocephalidae, which were recorded from multiple host groups within the region. Several other parasite families, including Quimperiidae, Allocreadiidae, and Echinostomatidae, were represented by fewer documented host associations. Fish families such as Anguillidae, Cobitidae, and Nemacheilidae were also associated with a range of parasite families, contributing to the diversity of reported host–parasite associations observed in the Marmara region. Overall, the network reflects the wide variety of documented host–parasite family associations reported from this region. In the Mediterranean region (Figure S2F), Cyprinidae was associated with more reported parasite families than most other host groups in the network. Frequently documented associations involved parasite families such as Dactylogyridae, Gyrodactylidae, Diplostomidae, Allocreadiidae, and Bothriocephalidae, which were recorded from multiple host groups within the region. Leuciscidae and several other fish families also contributed to the diversity of documented host–parasite associations observed in the Mediterranean dataset. In contrast, some parasite families, including Anguillicolidae and Trypanosomatidae, were represented by fewer documented associations and were recorded from relatively few host groups. Overall, the network summarizes the variety of host–parasite family associations reported from freshwater systems in the Mediterranean region. The Southeastern Anatolia network (Figure S2G) was considerably smaller than those of the other regions and included a single fish family, Cyprinidae, together with three parasite families: Dactylogyridae, Trichodinidae, and Lernaeidae. All documented associations in the regional dataset involved Cyprinidae, and no additional fish families were represented in the available records. As a result, the network consisted of only three documented host–parasite family associations.

3.3 | Cluster Analysis

The bipartite network, including all fish families (Figure 12) revealed noticeable differences in documented parasite diversity among the four identified clusters. Cluster C3 had the highest Shannon diversity value ($H' = 1.80$) and included several fish families associated with relatively high parasite diversity, particularly Leuciscidae and Cyprinidae. In contrast, Cluster C1 ($H' = 0.92$) was mainly associated with fish families with lower diversity values, including Alosidae, Gobiidae, Nemacheilidae, and Syngnathidae. Cluster C2 showed slightly lower diversity ($H' = 0.76$), whereas Cluster C4 had the lowest ($H' = 0.16$) among all clusters. The same general pattern was observed when only the 15 fish families with the highest

WF_Cluster x Fish Family bipartite network_all families (Shannon diversity)

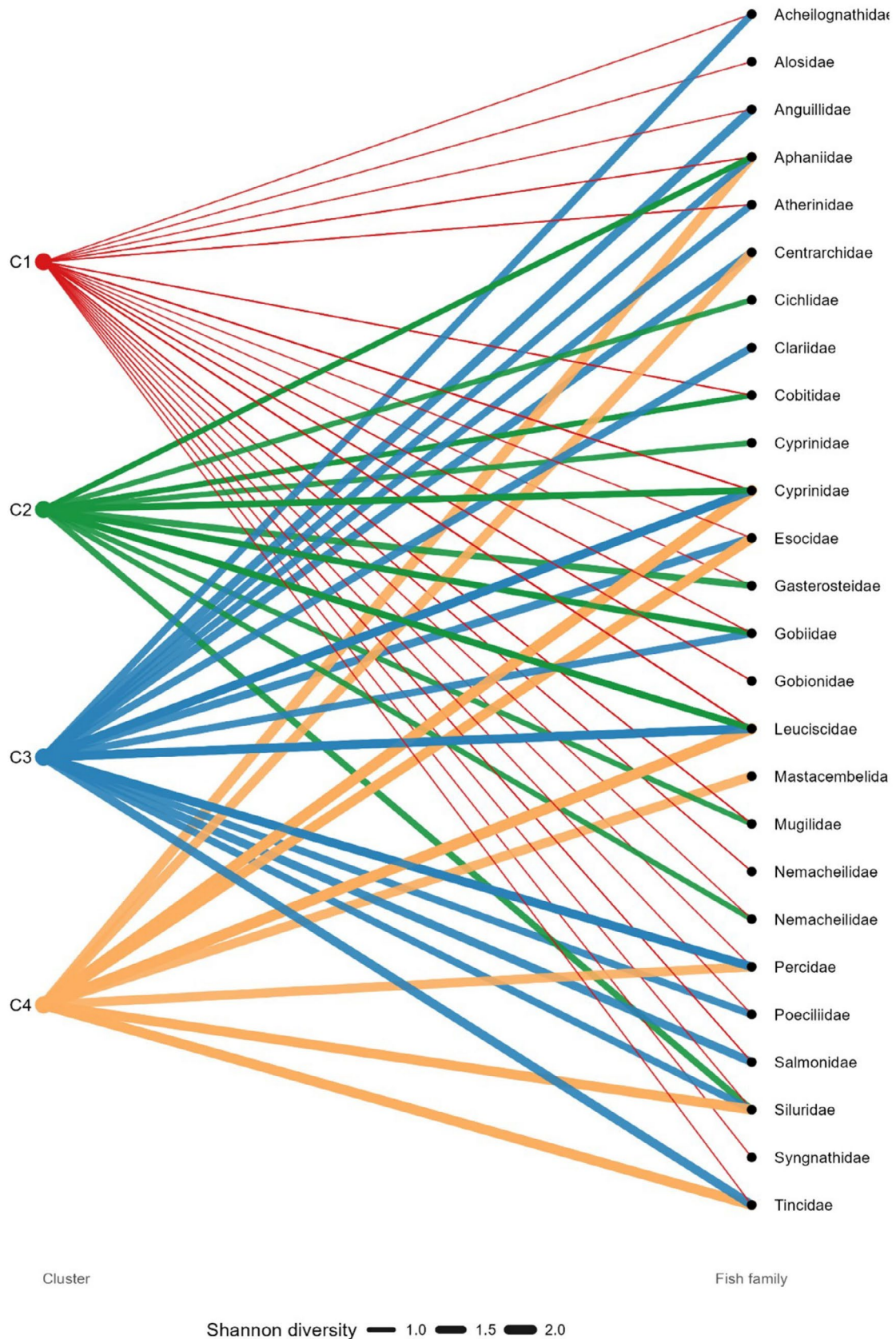


FIGURE 12 | Bipartite network showing the associations between the four clusters (C1–C4) and fish families, with edge thickness representing Shannon diversity values.

diversity values were considered (Figure S3), suggesting that the clustering results remained largely unchanged despite the reduced dataset. Overall, the clustering analysis highlights substantial variation in documented parasite diversity among freshwater fish families in Türkiye.

4 | Discussion

Bibliometric analysis is a systematic method for quantitatively assessing scientific literature within a particular research area (Hood and Wilson 2001). Since the early 2000s, the number of publications on fish parasites has increased both globally and in Türkiye, reflecting growing scientific interest in host–parasite interactions (Aguilar-Aguilar and Islas-Ortega 2015; Alves et al. 2017; Özer 2021, 2025; Ramallo and Ailán-Choke 2022; Chinh et al. 2023; Santos Reis et al. 2021; Wangchu et al. 2024; Araujo et al. 2025; Nagasawa and Chen 2025; Atroch et al. 2026). A temporary decline in publication output was observed around 2020, coinciding with the SARS-CoV-2 pandemic. Nevertheless, important gaps remain in long-term monitoring and in studies of understudied taxa and regions, highlighting the need for continued research on freshwater fish parasites.

This bibliometric survey, the first countrywide study, provided detailed data on parasites from diverse phyla, including Ciliophora, Platyhelminthes (Monogenea, Trematoda, and Cestoda), Cnidaria (Myxozoa), Nematoda, Arthropoda (Copepoda), Acanthocephala, and some minor taxa with fewer species. It also examined their interactions within wild freshwater fish hosts across seven geographical regions in Türkiye. The data show that the reported parasite species belonging to the above-mentioned taxa, along with the minor phyla Choanozoa, Myxozoa, Mollusca, Euglenozoa, and Annelida, were from 148 host fish species inhabiting these environments, representing approximately one-third of the 431 freshwater fish species reported from Türkiye (Froese and Pauly 2026). As shown in Figure 4, a total of 276 parasite species have been reported from freshwater fish hosts in Türkiye; however, it is not possible to determine the exact number of parasite species currently infecting host fish in those seven regions. This uncertainty largely reflects the fact that many studies focus on particular parasite groups rather than the complete parasite fauna of a host species, resulting in uneven documentation of parasite diversity. Limited taxonomic expertise, financial constraints, and restricted access to advanced identification techniques continue to limit comprehensive nationwide surveys (Poulin and Morand 2000; Poulin and Leung 2010; Özer 2022). Consequently, additional studies, particularly on unsurveyed host species, are needed to achieve a more complete understanding of parasite diversity in Turkish freshwater ecosystems.

In recent years, there has been growing concern about the global diversity and distribution of parasite richness, driven by increasing recognition of the ecological importance of parasites (Dougherty et al. 2016; Carlson et al. 2017). Although parasites are highly diverse in aquatic systems because of their long evolutionary history (Rohde 2005), the true richness of many macroparasitic groups, including acanthocephalans (Acanthocephala), tapeworms and flukes (Platyhelminthes), and roundworms (Nematoda), remains uncertain because of

statistical challenges, incomplete data on symbiont taxa, cryptic species, limited information on parasite occurrence in their hosts, and the shortage of parasite taxonomists (Price 1980; Brooks and Hoberg 2001; Poulin and Morand 2004; Nadler and Pérez-Ponce de León 2011; Poulin 2011; Carlson et al. 2020). Nevertheless, along with the above-mentioned parasitic taxa, ciliophorans (comprising trichodinids) and cnidarians (comprising myxozoans) are among the most common parasites of freshwater fish hosts (Kennedy 1974; Van As and Basson 1984; Salgado-Maldonado 2006; Kirjušina and Vismanis 2007; Djikanovic et al. 2012; Aguilar-Aguilar and Islas-Ortega 2015; Kabita et al. 2020). Among the parasite taxa documented in fish hosts from Turkish freshwater environments, Platyhelminthes accounted for the largest number of reported species in the present dataset ($n = 166$; 60.14%), followed by Nematoda ($n = 28$; 10.14%) and Ciliophora ($n = 20$; 7.25%). However, these patterns should be interpreted with caution, as differences in sampling effort, taxonomic expertise, and research focus among parasite groups may have influenced the number of species reported in the literature.

Factors influencing parasite species diversity across host groups have been widely investigated, and several host-related characteristics, including geographical distribution, diet, density, longevity, schooling behaviour, migration between freshwater and saltwater, ecology, evolution, and phylogeny, have all been associated with variation in parasite richness (Gregory 1990; Bell and Burt 1991; Aho and Bush 1993; Sasal et al. 1997; Poulin 1998; Poulin and Morand 1999; Morand et al. 2000; Desdevises 2006; Özer et al. 2016; Özer and Acar 2022). From the parasite perspective, different taxonomic groups are influenced by different ecological factors. Endoparasites, including acanthocephalans, trematodes, cestodes, and nematodes, have indirect life cycles and are often transmitted through food, making host diet an important driver of their diversity (Huston et al. 2020). In contrast, monogeneans and copepods are transmitted primarily through direct host contact, making host social behaviour more relevant to their distribution and species composition (Desdevises 2006). Host specificity also plays a key role in parasite ecology, with some parasites restricted to only a few host species, whereas others exploit a much broader host range (Euzet and Combes 1980; Poulin 1992). Together with host availability, environmental conditions, and transmission opportunities, these factors contribute to the observed patterns of parasite assemblages across host taxa and geographical regions. Nonetheless, host specificity varies considerably, even among closely related parasite species, so broad generalizations should be made with caution, particularly when based on family-level data. Parasite species richness is shaped by a combination of historical, biogeographical, environmental, and ecological factors (Poulin 1998; Poulin and Rohde 1997; Sasal et al. 1997). Among these, host geographical range appears to be especially important because widely distributed hosts are exposed to a greater variety of parasites (Aho and Bush 1993; Bell and Burt 1991; Thieltges et al. 2011; Kamiya et al. 2014; Poulin et al. 2020). This is particularly relevant to the present study, where parasite assemblages include taxonomic groups with contrasting life cycles and transmission strategies. The differences observed among host groups and geographical regions are therefore more likely to reflect the combined influence of several biological, ecological, and environmental factors than any single underlying process.

Across the seven geographical regions of Türkiye (Figures 6–9; Tables 1 and 2), the combined dataset included the largest number of fish families and showed the highest documented parasite-family diversity. The Marmara region followed the same pattern, whereas the Mediterranean region, despite having the second-highest fish-family richness, showed the lowest documented parasite-family richness. These differences probably reflect a combination of host diversity, environmental conditions, research effort, and the taxonomic focus of previous studies. The strong positive relationship between host-family reporting frequency and documented parasite-family richness (Spearman's $\rho=0.978$; Pearson's $r=0.900$) also suggests that research effort has influenced the observed diversity patterns. As a result, host families studied more frequently tended to have higher documented parasite-family richness, while additional surveys, particularly in less-studied regions, are likely to reveal parasite taxa that have not yet been recorded (Martin et al. 2012; Bellard and Jeschke 2016; Choudhury et al. 2016; Scholz et al. 2016; Özer 2022).

When parasite families were compared across geographical regions, the largest overlap was observed among those reported from all regions (Figure 8; Table 1), whereas many others were restricted to particular regions, indicating considerable geographical variation in parasite-family composition across Türkiye. A similar pattern was observed for host fish families. Cyprinidae and Leuciscidae were the only fish families reported from all regions and several regional combinations (Figure 9; Table 2), reflecting their broad geographical distribution in the available records. Likewise, parasite families such as Diplostomidae, Bothriocephalidae, Dactylogyridae, and Trichodinidae were documented in multiple regions. Although these findings suggest that some host and parasite families are widespread, the observed patterns should be interpreted cautiously because they may also reflect differences in research effort, host availability, and geographical coverage. Consequently, predicting parasite abundance remains difficult, as host–parasite associations are shaped by multiple interacting ecological and environmental factors (Williams et al. 2022).

Anthropogenic climate change poses an increasing challenge to the health and resilience of aquatic ecosystems (Atroch et al. 2026). Water temperature is a major driver of parasite distribution (Porter et al. 2024), and rising temperatures, together with changes in fish density, have been linked to shifts in parasite populations and host–parasite dynamics (Lanfranchi et al. 2024; Atroch et al. 2026). Thermal stress may favor certain parasite taxa by affecting their development, reproduction, and transmission, while also altering host immune responses and parasite prevalence. At the same time, environmental change can disrupt transmission pathways, particularly in parasites with complex life cycles (Atroch et al. 2026). Other environmental factors, including water-level fluctuations, flow regime changes, eutrophication, stratification, acidification, increased runoff, and extreme weather events, also influence host–parasite interactions in freshwater ecosystems (Marcogliese 2008).

Host specificity is a key aspect of parasite ecology because parasite species differ considerably in the range of hosts they exploit (Holt and Pickering 1985). However, host specificity can vary substantially even among closely related parasite taxa. Because the present study was conducted at the family level, the observed

patterns should be interpreted with caution, as closely related parasite species may differ markedly in their host ranges.

Understanding how parasites use different hosts provides insights into the evolutionary diversification of parasite lineages and the emergence of infectious diseases, although many factors underlying host use remain poorly understood (Lootvoet et al. 2013). Monogeneans and trematodes are among the most common parasites of bony fishes (Cribb et al. 2002), and a similar pattern was observed in the present study, where Platyhelminthes dominated the documented parasite diversity (Figure 4). Although these groups differ in their life histories and transmission strategies, both are widely represented in freshwater fish communities (Cribb et al. 2002). Host use and host specificity vary considerably among parasite species; therefore, broad generalizations based on family-level data should be avoided. As shown in Figure S1A, parasite families differed in the number of host families with which they were associated, although these patterns should be interpreted within the limitations of family-level analyses. Diplostomidae, Bothriocephalidae, Dactylogyridae, and Trichodinidae were consistently recorded across regions and network analyses, suggesting that they contributed substantially to the observed freshwater fish–parasite associations. Likewise, Cyprinidae and Leuciscidae were associated with numerous documented parasite families and were reported from most geographical regions included in this study. However, because the analyses were conducted at the family level, it remains unclear whether these patterns reflect broad host use across many species or are driven by a smaller number of widespread host or parasite species. Further studies using species-level data would provide a clearer understanding of these patterns, while regional differences may also reflect variation in research effort and available taxonomic expertise (Özer 2022).

In the present study, Figure 12 and Figure S3 illustrate the associations between the four identified clusters and host fish families from seven geographical regions of Türkiye. Leuciscidae, Cyprinidae, Siluridae, and Aphaniidae were generally associated with higher parasite diversity, whereas Cichlidae, Gobiidae, and Clariidae showed lower parasite diversity. These findings indicate substantial variation in documented parasite diversity among host fish families. However, because the analyses were based on published records and parasite diversity was summarized at the family level, the results should be interpreted with caution. Some of the observed variations may reflect differences in research effort among host groups, in addition to underlying biological and ecological factors. Further studies incorporating species-level data and broader geographical coverage would provide a more comprehensive understanding of parasite diversity in the freshwater fishes of Türkiye.

5 | Conclusion

Freshwater fish–parasite associations reported from the seven geographical regions of Türkiye reveal considerable diversity in both host and parasite taxa. The composition of documented parasite assemblages varied among regions and host families, highlighting substantial heterogeneity in reported host–parasite associations across the country. Although some of these patterns may reflect genuine biological differences among host groups, they

should also be interpreted in the context of unequal research effort, geographical coverage, and the family-level resolution of the compiled dataset. Despite these limitations, this study provides the first comprehensive synthesis of freshwater fish parasites across Türkiye and establishes a valuable baseline for future research. Further investigations, particularly those incorporating species-level data and focusing on understudied host groups and regions, will help improve our understanding of parasite diversity and host–parasite associations in Turkish freshwater ecosystems.

Author Contributions

A. Özer collected all data on parasites and freshwater hosts in Türkiye from previous publications and prepared them for statistical analyses. All statistical analyses on the data were conducted by N. Danacıoğlu, A. Yiğiter, and C. Hamurkaroglu. A. Özer prepared the first draft and final text of the manuscript. All authors reviewed the manuscript and provided edits on the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1A.** Reported associations between wild freshwater fish and parasite families in the Aegean Region. **Figure S1B.** Reported associations between wild freshwater fish and parasite families in the Black Sea Region. **Figure S1C.** Reported associations between wild freshwater fish and parasite families in the Central Anatolia Region. **Figure S1D.** Reported associations between wild freshwater fish and parasite families in the Eastern Anatolia Region. **Figure S1E.** Reported associations between wild freshwater fish and parasite families in the Marmara Region. **Figure S1F.** Reported associations between wild freshwater fish and parasite families in the Mediterranean Region. **Figure S2A.** Structure of the Wild Freshwater fish-parasite family network in the Aegean Region. **Figure S2B.** Structure of the Wild Freshwater fish-parasite family network in the Black Sea Region. **Figure S2C.** Structure of the Wild Freshwater fish-parasite family network in the Central Anatolia Region. **Figure S2D.** Structure of the Wild Freshwater fish-parasite family network in the Eastern Anatolia Region. **Figure S2E.** Structure of the Wild Freshwater fish-parasite family network in the Marmara Region. **Figure S2F.** Structure of the Wild Freshwater fish-parasite family network in the Mediterranean Region. **Figure S2G.** Structure of the Wild Freshwater fish-parasite family network in the Southeastern Anatolia Region. **Figure S3.** Bipartite network showing the associations between the four clusters (C1–C4) and fish families, with edge thickness representing Shannon diversity values.