

Diversity of freshwater fish in Jabodetabek (rivers and lakes), Indonesia

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Manuscript received: 22 October 2025. Revision accepted: 13 May 2026.

Abstract. *Ainy NS, Sjahfirdi L, Petala MP, Harinaldi. 2026. Diversity of freshwater fish in Jabodetabek (rivers and lakes), Indonesia. Biodiversitas 27 (5): d270518. <https://doi.org/10.13057/biodiv/d270518>.* In the Jabodetabek (Jakarta, Bogor, Depok, Tangerang and Bekasi) metropolitan area of Indonesia, this study assessed the structure of freshwater fish communities in interconnected river and lake ecosystems. The focus was on diversity, native-alien composition, and spatial homogenization along upstream-downstream river gradients and inlet-outlet lake zonation. From August to December 2024, fish were collected from three rivers (Ciliwung, Cisadane, and Cileungsi) and three lakes (Tonjong, Tunggilis, and Suradita) using standardized plots and various types of fishing gear. The data were then analyzed for species richness, abundance, diversity, dominance, PERMANOVA, and beta dispersion. Rivers had more species (38) and individuals (2,471) than lakes (27 species and 1,375 individuals), but they also had a higher proportion of alien fish (64.90%) than lakes (50.20%). *Oreochromis niloticus* and *Pterygoplichthys pardalis* were the dominant invasive species in rivers, especially in the middle and downstream sections. *Oreochromis niloticus* and *Amphilophus labiatus* were the dominant invasive species in lakes, particularly in inlet zones and disturbed areas. Lakes showed more pronounced cross-zone biotic homogenization, whereas rivers exhibited higher spatial turnover. However, some degraded areas also showed signs of homogenization. The findings suggest that biological invasions are reducing the complexity of Jabodetabek's freshwater ecosystems and pushing native species into less disturbed habitats. To reduce the risk of reinvasion and protect freshwater biodiversity, management should focus on controlling the most widespread invasive species, preventing new introductions, restoring habitats, and protecting existing native fish refuges.

Keywords: Alien fish, biotic homogenization, freshwater fish, urban freshwater ecosystems

INTRODUCTION

Freshwater ecosystems occupy only a small fraction of the Earth's surface but support disproportionately high biodiversity and ecosystem functioning (Strayer and Dudgeon 2010; Tickner et al. 2020). Their high heterogeneity and hydrological connectivity make them highly vulnerable to disturbance, placing them at the center of the freshwater biodiversity crisis, where biodiversity declines faster than in many terrestrial and marine systems (Dudgeon et al. 2006). Since the 1970s, freshwater fish populations have declined due to interacting pressures, including pollution, habitat degradation, flow modification, overexploitation, biological invasions, land-use change, climate change, and emerging contaminants (Reid et al. 2019; Tickner et al. 2020). Overall, freshwater fish loss is driven by the cumulative interaction of ecological, hydrological, chemical, and anthropogenic stressors.

Urbanization is a major source of ecological stress in freshwater ecosystems because it alters watershed hydrology, increases nutrient and pollutant inputs, simplifies habitat structure through channel modification and shoreline hardening, and disrupts river-lake connectivity (Walsh et al. 2005; Alberti 2015). These pressures interact and reinforce one another, accelerating biodiversity loss by reducing the resilience of sensitive native species and favoring generalist, disturbance-tolerant taxa (Grimm et al. 2008; McDonnell and Hahs 2015). As a

result, urban freshwaters often have fewer species, tolerant-taxa dominance, and more homogenized communities. Urbanization can also increase flow velocity, water temperature, pollutant inputs, salinization, and microplastic pollution, disrupting biological rhythms, species interactions, behavior, and reproduction (Antonelli et al. 2024; Lawson et al. 2024). In Southeast Asia, including Indonesia, habitat destruction, pollution, alien species, and rapid urban expansion have intensified threats to freshwater fish diversity (Hadiaty 2011; Albert et al. 2021). The Greater Jakarta area reflects this pattern: the Ciliwung, Cisadane, and Cileungsi rivers and connected lakes support fish habitats, drainage, water supply, and socio-economic needs, yet urban expansion increases pollution, sedimentation, channel modification, and riparian degradation, with downstream impacts spread through hydrological connectivity.

Research in West Java shows that fish communities in urban rivers generally follow a longitudinal pattern in which less disturbed upstream sections support more native species, whereas downstream sections exposed to stronger urban pressure are increasingly dominated by pollution-tolerant and alien taxa; this pattern has been documented in the Ciliwung and Cisadane Rivers (Hadiaty 2011; Sarifah et al. 2024; Mujadid et al. 2025), and reported in other Indonesian rivers such as the Cijalu, Cikawung, and Klawing Rivers (Nuryanto et al. 2015; Nuryanto et al. 2016; Suryaningsih et al. 2017). This pattern reflects a

modified river continuum, where land-use change, water-quality decline, and fragmented connectivity reshape ecological gradients and favor tolerant or alien species in stressed river segments (Vörösmarty et al. 2010; Grill et al. 2019). Biological invasions further worsen biodiversity loss in urban freshwaters. In Indonesia, over 50 alien fish species have been introduced into inland waters, with at least 14 considered invasive due to ecological impacts. Key examples include *Oreochromis niloticus*, which succeeds through broad tolerance, high reproduction, and flexible feeding (Canonica et al. 2005; Zengeya et al. 2015), and *Pterygoplichthys pardalis*, which tolerates hypoxic and polluted waters and can increase turbidity, weaken riverbanks, and damage spawning substrates through its burrowing activity (Chaichana and Jongphadungkiet 2012; Elfidasari et al. 2020); observations from the Ciliwung River further indicate that the increasing dominance of these invasive species is associated with declining native fish abundance (Sarifah et al. 2024).

In Jakarta, Bogor, Depok, Tangerang and Bekasi (Jabodetabek Area, Indonesia), invasive species pressure, declining water quality, sedimentation, and land-use change are reshaping freshwater fish assemblages, diversity (H'), evenness (E), and dominance (C). However, many Indonesian freshwater studies examine rivers and lakes separately, limiting understanding of invasion pressure,

habitat degradation, diversity, dominance, and biotic homogenization across interconnected urban river–lake systems (Reid et al. 2019; Lokatis and Jeschke 2022). This study evaluated freshwater fish communities across interconnected rivers and lakes in Jabodetabek by integrating river gradients and lake zonation. We hypothesized that invasive species increase in degraded downstream river segments, while urban lakes show lower diversity but higher evenness due to homogenization by tolerant and invasive taxa.

MATERIALS AND METHODS

Study area

This study was conducted in three major rivers in the West of Java, Indonesia, especially in Jakarta, Bogor, Depok, Tangerang and Bekasi (Jabodetabek): the Ciliwung, Cisadane, and Cileungsi. Each river was divided into upstream, middle, and downstream sections, yielding nine river sampling locations in total. Each lake was likewise divided into inlet, middle, and outlet zones, resulting in nine lake sampling locations. Sampling was conducted over five months, from August to December 2024. The sampling locations are shown in Figures 1 and 2, and Table 1.

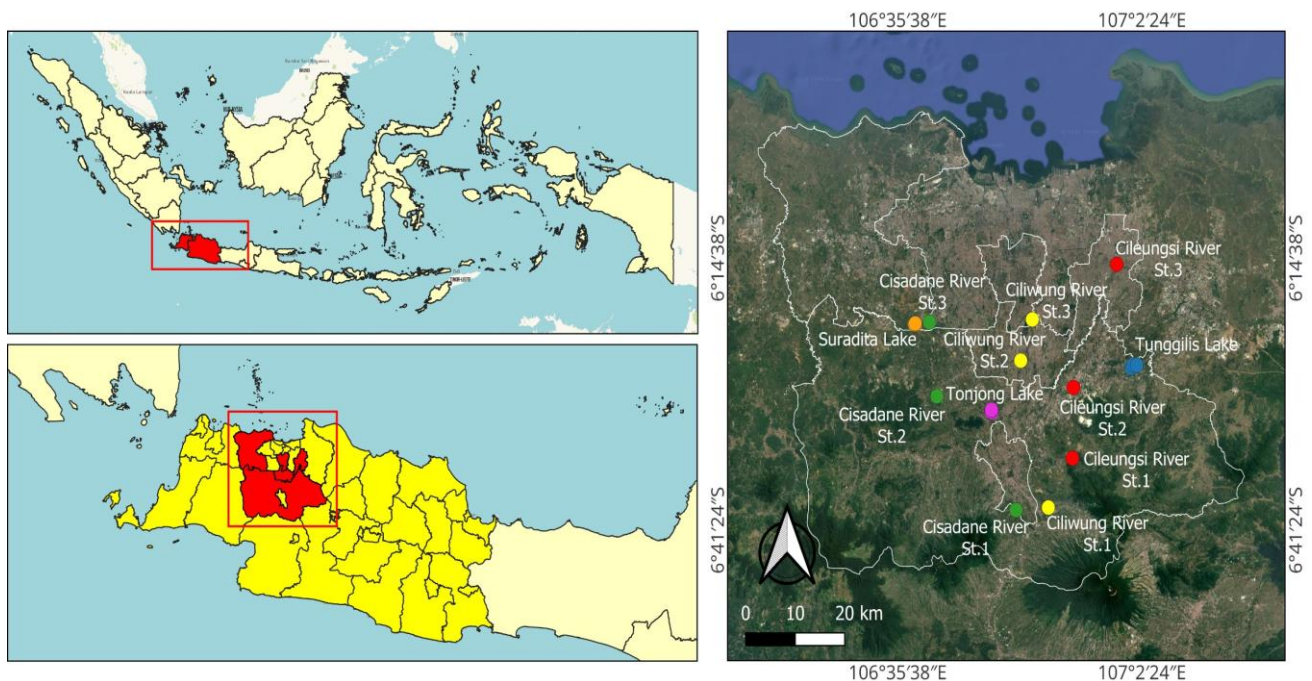


Figure 1. Sampling location in three rivers (Cisadane, Ciliwung, and Cileungsi) and three lakes (Suradita, Tonjong, Tunggilis), Jabodetabek Area, Indonesia

Table 1. Study site in Jabodetabek, West of Java, Indonesia

Station	Station name	Coordinate	Altitude (masl)
Ciliwung River			
St. 1	Gadog Bridge, Bogor	6°39'10.2"S 106°52'08.6"E	459
St. 2	Ciliwung Depok Community, Depok	6°24'42.7"S 106°49'06.7"E	75
St. 3	Ciliwung Bambon, Lenteng Agung, Jakarta	6°20'39.6"S 106°50'22.3"E	45
Cisadane River			
St. 1	Kampung Eretan, Cijeruk, Bogor	6°39'24.9"S 106°48'36.8"E	337
St. 2	Cisadane Valley, Ciseeng, Bogor	6°28'13.0"S 106°39'56.1"E	97
St. 3	Kranggan Tourism Village, Cisauk, Tangerang	6°20'55.1"S 106°39'06.8"E	23
Cileungsi River			
St. 1	Sentul Eco-Edu, Sentul, Bogor	6°34'18.8"S 106°54'47.0"E	310
St. 2	Pulekan, Nambo, Bogor	6°27'21.6"S 106°54'53.5"E	76
St. 3	Kalimalang, Bekasi	6°15'14.0"S 106°59'37.7"E	18
Tonjong Lake			
Plot 1	Tajurhalang, Bogor	6°29'48.0"S 106°45'57.7"E	141
Plot 2		6°29'41.8"S 106°45'50.4"E	137
Plot 3		6°29'32.8"S 106°45'54.8"E	140
Suradita Lake			
Plot 1	Cisauk, Tangerang, Banten	6°21'10.5"S 106°37'34.8"E	55
Plot 2		6°21'07.9"S 106°37'27.7"E	55
Plot 3		6°21'03.3"S 106°37'33.3"E	50
Tunggilis Lake			
Plot 1	Cibarusah, Bekasi	6°25'23.9"S 107°01'13.1"E	59
Plot 2		6°25'09.0"S 107°01'25.2"E	62
Plot 3		6°25'09.5"S 107°01'50.2"E	60



Figure 2. A. Geographic distribution of study sites representing upstream, middle, and downstream river segments as well as lake habitats within the Jabodetabek Area, Indonesia; B. Schematic illustration of fish sampling locations and longitudinal plot layout in lotic (river) ecosystems; and C. Schematic illustration of fish sampling locations and standardized littoral plot layout in lentic (lake) ecosystems

Procedures

Plot sampling design

In each river segment, an 80 m longitudinal plot was established with a width adjusted to the natural channel, whereas in lake (situ) ecosystems, a standardized 60 × 20 m littoral plot was placed along the shoreline contour. These dimensions were based on a preliminary species-area survey showing no additional species beyond 80 m in rivers and 60 × 20 m in lakes. Each plot was sampled three times between August and December 2024 to improve temporal consistency and reduce stochastic detection bias, following established freshwater fish survey practices that emphasize standardized sampling effort and temporal replication (Bonar et al. 2017). Repeated samples were treated as temporal observations within the same spatial unit rather than independent spatial replicates, so the results were interpreted primarily as site-specific descriptive patterns rather than broad regional statistical generalizations.

Fish sampling

Fish were sampled using four complementary gears-scoop nets, cast nets, rod fishing, and umbrella traps-to cover different habitats, size classes, and behavioral groups within standardized plots, namely 80 m longitudinal plots in rivers and 60 × 20 m littoral plots in lakes. Active gears were operated during the day (10:00-14:00 local time), whereas umbrella traps were deployed passively for a standardized soaking period. Scoop nets targeted small-bodied and juvenile fishes in shallow or vegetated margins (1 h per plot), cast nets sampled mobile open-water fishes (10 throws per plot over 1 h), rod fishing targeted medium-to large-bodied or predatory fishes using No. 5 hooks and earthworm bait (2 h per plot), and umbrella traps were used mainly in lakes, with five baited traps set at 1-1.5 m depth for 12 h. Sampling effort was standardized within each gear type to estimate Catch Per Unit Effort (CPUE), but because gears differed in selectivity and capture efficiency, CPUE was used descriptively to indicate relative abundance and dominance within habitats rather than for direct comparisons among gears. As sampling covered a limited seasonal period, the results were interpreted as a spatial snapshot of fish community structure rather than a representation of full seasonal variation. Nevertheless, active and passive gears were combined to improve species detectability and reduce gear-specific sampling bias across heterogeneous urban freshwater habitats (Ricker 1975).

Data identification, verification, and specimen handling

All captured fish were identified to the species level using standard Southeast Asian freshwater fish identification keys (Kottelat and Whitten 1996). Taxonomic verification was supported by expert consultation. Specimens were photographed alive immediately after capture to document diagnostic morphological characters. Voucher specimens were retained only when necessary for taxonomic confirmation (1-3 individuals per species) and deposited in the STKIP

Arrahmaniyah Ichthyology Collection, Indonesia, to ensure traceability (Mujadid and Ainy 2025).

Data analysis and standardized metrics (H' , E , C , and CPUE)

Community structure was evaluated using the Shannon-Wiener Diversity Index (H'), Evenness Index (E), and Simpson Dominance Index (C), calculated as:

$$\begin{aligned} H' &= -\sum p_i \ln(p_i) \\ E &= H' / \ln(S) \\ C &= \sum p_i^2 \end{aligned}$$

Where, p_i is the proportion of individuals in species i and S is species richness.

Abundance was standardized using Catch Per Unit Effort (CPUE), calculated as: CPUE = The total number of individuals / the total standardized fishing effort per plot, following widely adopted fisheries assessment approaches (Ricker 1975; Bonar et al. 2017). All indices (H' , E , C), count data, abundance, local distribution, and CPUE values were further analyzed to assess invasion potential and dominance patterns under anthropogenic disturbance, following frameworks in invasion ecology (Moyle and Marchetti 2006; Gozlan et al. 2010).

RESULTS AND DISCUSSION

Species richness and taxonomic composition

A total of 38 freshwater fish species from 18 families and 7 orders were recorded in the Ciliwung, Cisadane, and Cileungsi Rivers, with Cyprinidae as the richest family (10 species), followed by Bagridae, Cichlidae, and Poeciliidae (three species each) (Table 2). Despite this diversity, abundance was highly uneven: five species—*O. niloticus*, *P. pardalis*, *Rasbora aprotaenia*, *Gambusia affinis*, and *Poecilia reticulata*—accounted for 67.7% of all individuals, indicating strong dominance by a few taxa (Figure 3). Alien fishes were represented by several families, showing that non-native taxa were taxonomically diverse rather than confined to a single lineage. Among the five most abundant species, only *R. aprotaenia* was native, whereas many other taxa occurred at low abundance and were restricted to a few river segments (Table 2).

In contrast, lake assemblages comprised 27 freshwater fish species from 17 families, with Cyprinidae contributing the highest species richness (4 species), while Cichlidae and Osphronemidae contributed substantially to total abundance (Table 3). Lake assemblages were numerically dominated by cichlids, especially *O. niloticus* and *Amphilophus labiatus*, which occurred consistently across all sampled lakes (Figure 4). Alien fishes were represented by several families, but their numerical dominance was centered mainly on cichlids. Several native species, such as *Trichopsis vittata*, *Trichogaster trichopterus*, and *Aplocheilichthys armatus*, also showed relatively high abundance and broad distributions.

Table 2. Species composition of Ciliwung River, Cisadane River, and Cileungsi River, West of Java, Indonesia

Species	Ciliwung			Cisadane			Cileungsi			Total (ind.)	Abund (ind./St.)	Loc dist (%)	Status	Potential
	1	2	3	1	2	3	1	2	3					
Family Cyprinidae														
<i>Hampala macrolepidota</i> Kuhl & Van Hasselt, 1823	0	33	1	4	6	3	0	0	0	47	9.40	55.56	N	O
<i>Mystacoleucus marginatus</i> (Valenciennes, 1842)	0	14	0	0	0	15	3	91	0	123	30.75	44.44	N	C
<i>Barbodes binotatus</i> (Valenciennes, 1842)	26	9	0	22	14	12	1	9	0	93	13.29	77.78	N	C
<i>Osteochillus vittatus</i> (Valenciennes, 1842)	0	1	0	0	0	0	0	0	0	1	1.00	11.11	N	C
<i>Barbonymus balleroides</i> (Valenciennes, 1842)	0	1	0	1	0	4	0	9	0	15	3.75	44.44	N	C
* <i>Cyprinus carpio</i> Linnaeus, 1758	1	0	1	0	0	0	0	0	0	2	1.00	22.22	A	C
<i>Lobocheilos falcifer</i> (Valenciennes, 1842)	0	0	0	0	4	0	0	0	0	4	4.00	11.11	N	O
<i>Barbonymus gonionotus</i> (Bleeker, 1849)	0	0	0	0	0	4	0	0	0	4	4.00	11.11	N	C
<i>Neolissochilus soro</i> (Valenciennes, 1842)	8	0	0	0	0	0	0	0	0	8	8.00	11.11	N	O
Family Danionidae														
<i>Rasbora aprotaenia</i> Hubbs & Brittan, 1954	8	2	0	22	4	5	139	30	0	210	30.00	77.78	N	C
Family Cobitidae														
<i>Pangio oblonga</i> (Valenciennes, 1846)	7	7	0	3	0	0	0	1	0	18	4.50	44.44	N	O
<i>Pangio doriae</i> (Perugia, 1892)	0	31	0	0	0	0	0	0	0	31	31.00	11.11	N	O
Family Balitoridae														
<i>Nemacheilus fasciatus</i> (Valenciennes, 1846)	6	0	0	6	0	0	5	4	0	21	5.25	44.44	N	O
<i>Lepidocephalichthys hasseltii</i> (Valenciennes, 1846)	0	0	0	0	49	0	0	0	0	49	49.00	11.11	N	O
Family Gyrinocheilidae														
* <i>Gyrinocheilus aymonieri</i> (Tirant, 1883)	0	0	0	0	1	0	0	0	0	1	1.00	11.11	A	O
Family Bagridae														
<i>Hemibagrus nemurus</i> (Valenciennes, 1840)	0	35	22	17	6	5	0	1	0	86	14.33	66.67	N	C
<i>Hemibagrus planiceps</i> (Valenciennes, 1840)	1	0	0	6	2	0	1	0	0	10	2.50	44.44	N	C
<i>Mystus singaringan</i> (Bleeker, 1846)	0	47	4	1	3	0	0	0	0	55	13.75	44.44	N	C
Family Clariidae														
* <i>Clarias batrachus</i> (Linnaeus, 1758)	0	3	1	0	0	0	0	0	0	4	2.00	22.22	A	C
* <i>Clarias gariepinus</i> (Burchell, 1822)	0	0	0	0	0	0	0	1	0	1	1.00	11.11	A	C
Family Loricariidae														
* <i>Pterygoplichthys pardalis</i> (Castelnau, 1855)	2	14	54	7	5	4	0	212	134	432	61.71	77.78	A	O
* <i>Ancistrus temminckii</i> (Valenciennes, 1840)	24	1	2	33	1	0	55	3	0	119	17.00	77.78	A	O
Family Sisoridae														
<i>Glyptothorax platypogon</i> (Valenciennes, 1840)	8	9	0	6	0	1	0	0	0	24	6.00	44.44	N	O
Family Cichlidae														
* <i>Oreochromis niloticus</i> (Linnaeus, 1758)	3	19	24	59	73	10	2	474	0	664	83.00	88.89	A	C
* <i>Andinoacara rivulatus</i> (Günther, 1860)	2	0	0	0	0	0	0	0	0	2	2.00	11.11	A	O
* <i>Amphilopus labiatus</i> (Günther, 1864)	0	0	1	1	0	0	0	0	0	2	1.00	22.22	A	O
Family Mastembelidae														
<i>Mastacembelus unicolor</i> Cuvier, 1832	0	0	0	0	3	0	0	0	0	3	3.00	11.11	N	O
<i>Macrogathus maculatus</i> (Cuvier, 1832)	0	10	0	22	4	3	0	0	0	39	9.75	44.44	N	O
Family Synbranchidae														
<i>Monopterus albus</i> (Zuiew, 1793)	0	2	1	0	0	0	0	0	0	3	1.50	22.22	N	C

<i>*Gambusia affinis</i> (Baird & Girard, 1853)	0	2	1	11	0	0	12	4	0	30	6	44.44	A	FF
<i>*Poecilia reticulata</i> Peters, 1859	0	0	3	0	0	0	0	0	0	3	3	11.11	A	O
Family Zenarchopteridae														
<i>Dermogenys pussila</i> Kuhl & van Hasselt, 1823	10	2	10	0	0	0	2	0	0	24	6	44.44	N	NI
Family Anabantidae														
<i>Anabas testudineus</i> (Bloch, 1792)	0	2	0	0	0	0	0	0	0	2	2	11.11	N	C
Family Osphronemidae														
<i>Trichogaster trichopterus</i> (Pallas, 1770)	2	3	2	31	5	53	13	2	6	117	13	100	N	O
<i>Trichopsis vittata</i> (Cuvier, 1831)	43	11	3	44	4	22	31	14	20	192	21.33	100	N	O
Family Channidae														
<i>Channa striata</i> (Bloch, 1793)	4	1	0	0	0	1	0	0	0	6	2	33.33	N	O
<i>Channa lucius</i> (Cuvier, 1831)	10	1	0	55	0	0	0	0	0	66	22	33.33	N	O
Family Butidae														
<i>Oxyeleotris marmorata</i> (Bleeker, 1852)	1	0	0	1	0	0	3	0	4	9	2.25	44.44	N	C
Family Oxudercidae														
<i>Brachygobius xanthomelas</i> Herre, 1937	0	0	0	0	0	0	4	0	4	8	4	22.22	N	O
<i>Gobiopterus chuno</i> (Hamilton, 1822)	0	2	0	0	0	0	0	0	0	2	2	11.11	N	O
Family Ambassidae														
<i>*Parambassis siamensis</i> (Fowler, 1937)	26	12	0	7	0	0	1	0	0	46	11.5	44.44	A	O
Family Adrianichthyidae														
<i>Oryzias hubbsi</i> Roberts, 1998	1	122	0	34	0	3	0	0	0	160	40	44.44	N	O

Note: 1. Inlet, 2. Middle, 3. Outlet, Abund: Abundance, Loc dist: Local distribution, C: Consume fish, O: Ornamental fish, FF: Feeding Fish, N: Native, A: Alien, *: Alien fish

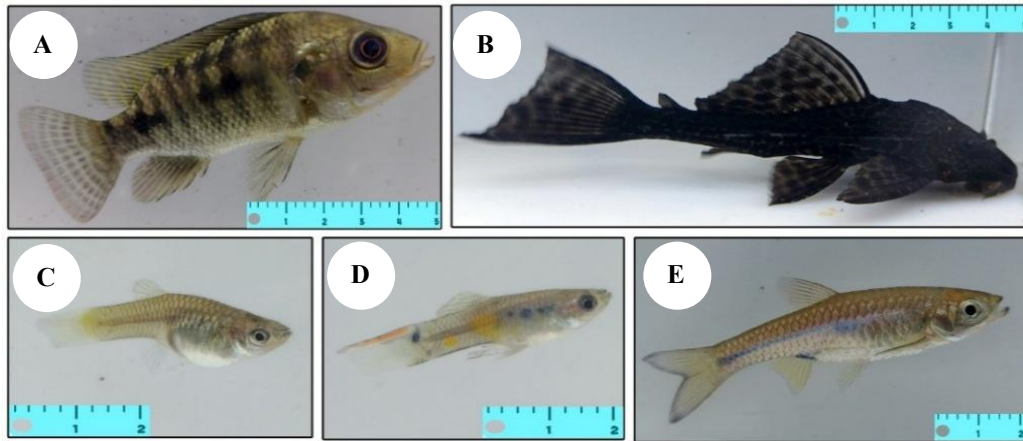


Figure 3. The five largest species in rivers (Ciliwung, Cileungsi, and Cisadane in West of Java, Indonesia). Note: A. Nile Tilapia (*Oreochromis niloticus*), B. Common Pleco (*Pterygoplichthys pardalis*), C. Mosquito Fish (*Gambusia affinis*), D. Guppy (*Poecilia reticulata*), and E. Java Rasbora (*Rasbora aprotaenia*)

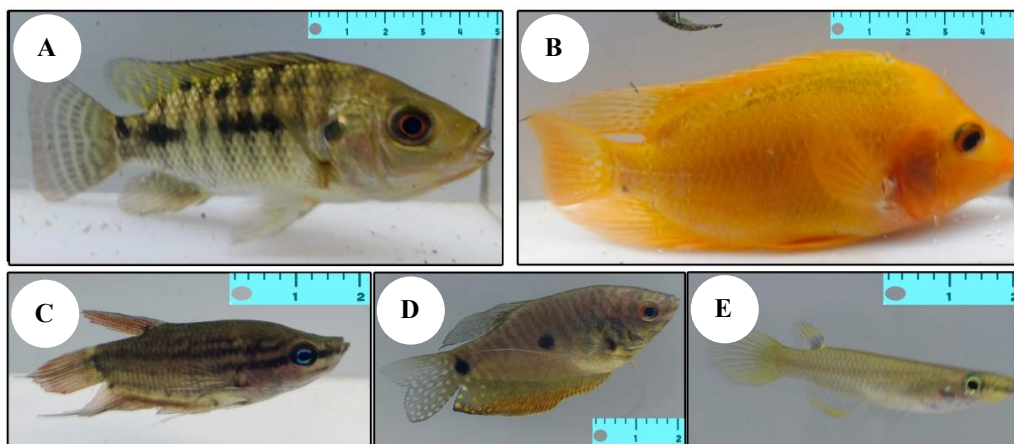


Figure 4. The five largest species in lakes (Tonjong, Tunggilis, Suradita in West of Java, Indonesia). Note: A. Nile Tilapia (*O. niloticus*), B. Midas cichlid (*Amphilophus labiatus*), C. Croaking gouramy (*Trichopsis vittata*), D. Three-spot gouramy (*Trichogaster trichopterus*), and E. *Aplocheilichthys armatus*

Native and alien species dominance patterns

Across all sampling sites, fish assemblages showed marked variation in the proportional contribution of native and alien taxa among river segments and lake sites (Figures 5-6). Rivers supported a higher proportion of alien fishes (64.90%) than lakes (50.20%) (Table 4). The dominant alien taxa also differed between habitats: in rivers, alien dominance was driven mainly by *O. niloticus*, *P. pardalis*, *Ancistrus temminckii*, *G. affinis*, and *P. reticulata*, whereas in lakes it was associated primarily with *O. niloticus* and cichlids such as *A. labiatus* (Table 4; Figure 6). This indicates that alien dominance was stronger and taxonomically broader in rivers than in lakes. The higher Dominance Index in rivers ($C = 0.40$) than in lakes ($C = 0.33$) further shows that river assemblages were more uneven and more strongly concentrated around a few dominant alien taxa (Table 4).

Cileungsi showed a distinct pattern of low diversity and high abundance, reflected in the low H' values in Table 5 and high fish abundance in Figure 6. Across ecosystems, *O. niloticus* was the most consistently abundant alien species. In rivers, alien fishes, especially *O. niloticus* and *P.*

pardalis, were concentrated in the middle and downstream sections, whereas native cypriniforms were more prominent upstream (Table 2). In lakes, alien abundance was highest in the inlet zone, driven mainly by *O. niloticus*, while native fishes were dominated by anabantiforms (Table 3). Overall, rivers had higher richness and abundance than lakes, but also a greater alien component and stronger dominance by a few taxa (Table 4).

Spatial variation in diversity indices

Table 5 shows stronger spatial variation in fish community structure in rivers than in lakes. In rivers, H' generally declined downstream and C increased, most sharply in Cileungsi (H' 1.06 to 0.46; C 0.48 to 0.75). Similar but weaker trends occurred in Ciliwung and Cisadane. In lakes, zonal variation was smaller, except in Tonjong, where H' declined from 1.91 at the inlet to 1.05 at the outlet, and C increased from 0.20 to 0.48. Overall, river assemblages showed a clearer downstream shift toward lower diversity and higher dominance than lake assemblages (Table 5).

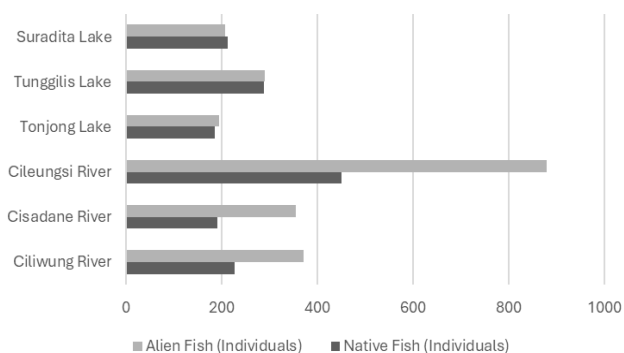


Figure 5. Comparison of the proportion of native and alien freshwater fishes between lakes and rivers in Jabodetabek, Indonesia

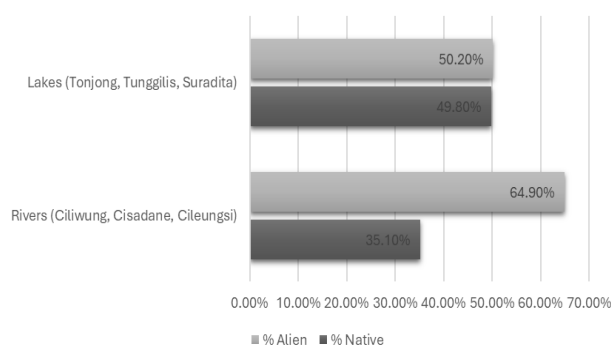


Figure 6. Comparison of native and alien fish abundance across freshwater sites in Jabodetabek, Indonesia

Table 4. Comparison of fish community characteristics between river and lake habitats in Jabodetabek, Indonesia

Parameter	Rivers (Ciliwung, Cileungsi, Cisadane)	Lakes (Tonjong, Tunggilis, Suradita)
Number of species (S)	38	27
Total abundance (N)	2,471	1375
Native abundance	867	639
Alien abundance	1,604	736
Proportion alien (%)	64.90%	50.20%
Diversity Index (H')	1.46	1.24
Evenness (E)	0.62	0.88
Dominance Index (C)	0.40	0.33
Dominant native species	<i>Rasbora aprotaenia, Mystacoleucus marginatus, Barbodes binotatus</i>	<i>Trichogaster trichopterus, Trichopsis vittata, Aplocheilichthys armatus, Channa lucius</i>
Dominant alien species	<i>Oreochromis niloticus, Pterygoplichthys pardalis, Ancistrus temminckii, Gambusia affinis, Poecilia reticulata</i>	<i>Oreochromis niloticus, Amphiphophus labiatus</i>

Table 5. Values of Diversity Index (H'), Uniformity Index (E), and Dominance Index (C)

Rivers	Index	Upstream	Middle	Downstream	Lakes	Index	Inlet	Middle	Outlet
Ciliwung	H'	1.93	2.1	1.33	Tonjong	H'	1.91	1.4	1.05
	E	0.58	0.83	0.47		E	0.81	0.73	0.67
	C	0.18	0.15	0.34		C	0.20	0.35	0.48
Cileungsi	H'	1.06	1.4	0.46	Tunggilis	H'	1.46	1.11	1.24
	E	0.57	0.68	0.42		E	0.71	0.77	0.75
	C	0.48	0.33	0.75		C	0.33	0.41	0.36
Cisadane	H'	1.92	1.56	1.47	Suradita	H'	1.41	1.25	1.35
	E	0.77	0.69	0.84		E	0.74	0.79	0.77
	C	0.20	0.32	0.30		C	0.35	0.37	0.35

Consistent with Table 5, the pooled summary in Table 6 shows a stronger spatial gradient in rivers than in lakes. In rivers, mean Shannon-Wiener Diversity Index (H') was highest in the middle segment (1.723±0.443), slightly lower upstream (1.639±0.503), and declined sharply downstream (1.089±0.618), accompanied by lower evenness and higher dominance. In lakes, the same trend occurred but was weaker, with H' decreasing from inlet to outlet (1.592±0.377 to 1.212±0.329), along with lower evenness and higher dominance. Overall, both ecosystems showed lower diversity and higher dominance toward downstream or outlet sections, but the shift was more pronounced in rivers (Table 6).

Table 7 shows significant among-station variation in Shannon-Wiener diversity (H'; F = 3.133, p = 0.001941)

and dominance (C; F = 2.439, p = 0.012088), but not in evenness (E; F = 1.527, p = 0.140302). This indicates that spatial heterogeneity was expressed more clearly in diversity and dominance than in evenness (Table 7).

Table 8 shows a significant shift in alien and native fish contributions across spatial units. In rivers, native fish dominated upstream (71.77%), whereas alien fish dominated the middle and downstream segments (60.23% and 62.94%), indicating a longitudinal shift from native- to alien-dominated communities. The middle segment also had the highest total abundance (1,418 individuals), coinciding with the strongest numerical contribution of alien fish. In lakes, the pattern was reversed, with alien fish dominating the inlet zone (62.02%) and native fish dominating the middle and outlet zones (Table 8).

Table 6. Alpha diversity indices of fish communities across lake and river ecosystems

Ecosystem	Zone / Segment	H' (Mean±SD)	E (Mean±SD)	C (Mean±SD)	n
Lake	Inlet	1.592±0.377	0.770±0.134	0.292±0.129	9
Lake	Middle	1.253±0.433	0.745±0.112	0.376±0.133	9
Lake	Outlet	1.212±0.329	0.666±0.157	0.397±0.156	9
River	Upstream	1.639±0.503	0.746±0.162	0.288±0.181	9
River	Middle	1.723±0.443	0.739±0.137	0.268±0.141	9
River	Downstream	1.089±0.618	0.589±0.236	0.467±0.275	9

Table 7. One-way ANOVA results for fish diversity indices among stations

Variable	Between-group SS	df	Mean Square	F-value	p-value	Interpretation
Shannon-Wiener Diversity Index (H')	7.942	17	0.467	3.133	0.001941	Significant difference
Evenness Index (E)	0.548	17	0.032	1.527	0.140302	Not significant
Dominance Index (C)	0.946	17	0.056	2.439	0.012088	Significant difference

Temperature, pH, and TDS also varied widely across sites, with TDS generally increasing downstream or toward outlet zones. ANOVA confirmed significant among-segment differences in DO, pH, temperature, TDS, NH₃, dKH, and chlorine, whereas NO₂, NO₃, and hardness did not differ significantly. Overall, spatial heterogeneity was strongest for key water-quality parameters, particularly DO, pH, and TDS (Table 9).

Gear-specific capture outcomes

Table 10 shows clear variation in capture efficiency among sampling gears, with scoop nets being the most effective for recovering overall fish abundance, followed by cast nets, whereas rod fishing and umbrella traps yielded much lower catch rates. These differences indicate that each gear sampled different components of the fish assemblage, so CPUE should be interpreted as gear-specific descriptive information rather than as a direct measure of equivalence among gears.

Fish community spatial variation and homogenization

PERMANOVA based on Bray-Curtis dissimilarity showed significant spatial differences in fish community composition in both habitat types (Table 11). Lake assemblages differed among inlet, middle, and outlet zones (Pseudo-F = 3.1462, $p < 0.0001$), whereas river assemblages showed stronger separation among upstream, middle, and downstream segments (Pseudo-F = 4.4830, $p < 0.0001$). Overall, spatial position significantly structured fish assemblages in both lentic and lotic systems, with a stronger pattern in rivers.

Beta-dispersion analysis showed marked variation in fish community homogenization among waterbodies and spatial units (Table 12). The Cileungsi River showed consistently high homogenization across all segments, indicated by low mean distances to the centroid upstream (0.203), middle (0.289), and downstream (0.237). In contrast, Ciliwung showed intermediate homogenization,

whereas Cisadane remained more heterogeneous, especially downstream (0.611). In lakes, high homogenization occurred at the Tunggilis inlet and middle zone and at the Suradita outlet, while Tonjong was less homogenized overall. These results indicate that homogenization was shaped not only by ecosystem type but also by individual waterbodies and spatial units, with the most consistent pattern occurring in Cileungsi (Table 12).

Table 8. Proportion of alien and native fish individuals across river segments and lake zones

Ecosystem	Zone / Segment	Alien (%)	Native (%)	Total individuals
River	Upstream	28.23	71.77	659
River	Middle	60.23	39.77	1418
River	Downstream	62.94	37.06	394
Lake	Inlet	62.02	37.98	761
Lake	Middle	38.80	61.20	250
Lake	Outlet	37.64	62.36	364

Table 9. Summary of one-way ANOVA of water quality parameters among sampling segments

Parameters	F-value	P-value
DO (ppm)	25.131	<0.001*
Temperature (°C)	2.969	0.026*
pH	13.236	<0.001*
TDS (ppt)	24.792	<0.001*
NH ₃	15.625	<0.001*
NO ₂	1.667	0.175ns
NO ₃	2.123	0.088ns
dKH	3.950	0.007*
Hardness	1.500	0.225ns
Chlorine	4.446	0.004*

Table 10. Gear-specific Catch Per Unit Effort (CPUE) of freshwater fish assemblages based on standardized within-gear sampling effort

Fishing gear	Total catch (individuals)	Standardized effort per plot	CPUE	Unit
Scoop nets	2,161	1 h	40.02	ind·h ⁻¹ ·plot ⁻¹
Cast nets	660	1 h (10 throws)	12.22	ind·h ⁻¹ ·plot ⁻¹
Rod fishing	479	2 h	4.43	ind·h ⁻¹ ·plot ⁻¹
Umbrella traps	546	12 h (5 traps = 60 trap hours)	0.17	ind·h ⁻¹ ·plot ⁻¹

Note: CPUE was calculated separately for each fishing gear using standardized within-gear effort per plot. Because gears differed in selectivity, capture efficiency, target groups, and deployment duration, CPUE was interpreted descriptively within each gear rather than compared directly among gears. Values represent mean catch per plot based on 18 sampling plots with three replicates (n = 54 plot-efforts)

Table 11. PERMANOVA results for fish community composition based on Bray-Curtis dissimilarity

Ecosystem	Factor	df	Pseudo-F	p-value	Interpretation
Lake	Zone (Inlet, Middle, Outlet)	2	31.462	0.0001	Significant difference
River	Segment (Upstream, Middle, Downstream)	2	44.830	0.0001	Significant difference

Note: PERMANOVA was performed using Bray-Curtis distances with 9,999 permutations. Significant p-values (< 0.05) indicate statistically distinct fish community compositions among zones/segments within each ecosystem

Table 12. Beta-dispersion values by ecosystem, zone/segment, location, and relative homogenization category

Ecosystem	Zone / Segment	Location	Mean distance to centroid	Homogenization level
River	Upstream	Cileungsi	0.203	High
River	Middle	Cileungsi	0.289	
River	Downstream	Cileungsi	0.237	
Lake	Inlet	Tunggilis	0.307	
Lake	Middle	Tunggilis	0.216	
Lake	Outlet	Suradita	0.263	
River	Upstream	Ciliwung	0.363	Intermediate
River	Middle	Ciliwung	0.371	
River	Downstream	Ciliwung	0.330	
Lake	Inlet	Suradita	0.331	
Lake	Outlet	Tonjong	0.354	
Lake	Outlet	Tunggilis	0.395	
River	Upstream	Cisadane	0.427	Low
River	Middle	Cisadane	0.438	
River	Downstream	Cisadane	0.611	
Lake	Inlet	Tonjong	0.399	
Lake	Middle	Tonjong	0.441	
Lake	Middle	Suradita	0.398	

Note: Homogenization level was classified relative to the observed beta dispersion values across all 18 groups. Lower mean distance to centroid indicates greater compositional similarity among replicate assemblages and thus stronger biotic homogenization. Groups were classified as High homogenization when beta dispersion was ≤ 0.322 , Intermediate when > 0.322 to ≤ 0.396 , and Low homogenization when > 0.396

Discussion

Longitudinal patterns of diversity and alien dominance

The heatmap in Figure 7 strengthens the longitudinal results by showing that dominant alien and native fishes were not distributed evenly across river and lake gradients. Alien species, particularly *O. niloticus* and *P. pardalis*, were highly abundant in middle and downstream river segments and remained widely distributed across lake zones, whereas native species were generally more localized in upstream river sections or specific lake habitats. This visual pattern is consistent with the quantitative results in Tables 6-9, where river fish assemblages shifted toward lower diversity and higher alien dominance downstream. Shannon-Wiener Diversity Index (H') declined from 1.639 ± 0.503 upstream to 1.089 ± 0.618 downstream, while dominance (C) increased from 0.288 ± 0.181 to 0.467 ± 0.275 (Table 6), and ANOVA confirmed significant among-station differences in both

indices (Table 7). Table 8 further shows a clear invasion gradient, with alien individuals increasing from 28.23% upstream to 60.23% in the middle segment and 62.94% downstream. Together, these findings indicate ecological filtering under disturbance pressure rather than natural succession, consistent with the urban stream syndrome framework and recent evidence from the Ciliwung River (Walsh et al. 2005; Mujadid et al. 2025). Within the Jabodetabek metropolitan landscape, this pattern is important because rivers are not isolated ecological units, but parts of connected urban freshwater systems through which environmental stress and invasion pressure can spread to associated lentic habitats. The repeated dominance of adaptable alien taxa reflects their broad environmental tolerance, strong establishment potential, and resilience in disturbed freshwater habitats, which may give them a competitive advantage over more sensitive native species in degraded environments (Chaichana and

Jongphadungkiet 2012; Wei et al. 2017). This interpretation aligns with trait-based invasion theory, which suggests that tolerance-related life-history traits facilitate establishment and competitive success in degraded habitats (Moyle and Marchetti 2006). Overall, Figure 7 and Tables 6-9 indicate that downstream fish communities were more simplified and dominated by a few alien, disturbance-tolerant species, whereas upstream assemblages remained more diverse and native-dominated, reflecting ecological homogenization under urban disturbance (Olden 2006).

Homogenization in lake ecosystems

PERMANOVA analysis revealed that the composition of the fish community varied among the lake zones (Pseudo-F = 3.1462, p < 0.0001), suggesting that zonal structure was still discernible (Table 11). However, the beta dispersion analysis revealed that homogenization did not occur universally across the lakes (Table 12). This interpretation is further substantiated by Table 13, which summarizes the dominant and ecologically significant species that influence river and lake assemblages in Jabodetabek. The species are categorized according to their abundance, local distribution, native-alien status, spatial occurrence, and inferred contribution to community patterns. The table demonstrates that alien taxa, specifically *O. niloticus*, *P. pardalis*, *A. labiatus*, *G. affinis*, and *P. reticulata*, significantly contributed to alien dominance,

reduced evenness, assemblage simplification, and community homogenization. In contrast, native species such as *R. aprotaenia*, *T. vittata*, *T. trichopterus*, *A. armatus*, and *Oryzias hubbsi* represented residual native species. High homogenization was recorded in the Tunggilis inlet and middle zones and the Suradita outlet, whereas Tonjong and the Suradita middle zone remained less homogenized. Together, these patterns indicate that homogenization developed locally where assemblages became dominated by a few widespread tolerant taxa, especially *O. niloticus*, reducing compositional distinctiveness and leaving only a smaller subset of native species across zones. This pattern was most evident in Tonjong, where the outlet showed a more simplified assemblage, consistent with biotic homogenization under persistent disturbance and habitat simplification in urban freshwater systems (Olden 2006; Rahel and Olden 2008). In connected urban freshwater systems, this pattern is especially relevant in inlet zones, where lakes receive cumulative pressures from surrounding catchments and adjacent flowing waters, increasing the likelihood of assemblage convergence under repeated disturbance. Once such dominance is established, sensitive native taxa may have fewer opportunities to recolonize, reinforcing the view that lentic habitats can become invasion-prone under disturbance pressure (Gozlan et al. 2010; Havel et al. 2015).

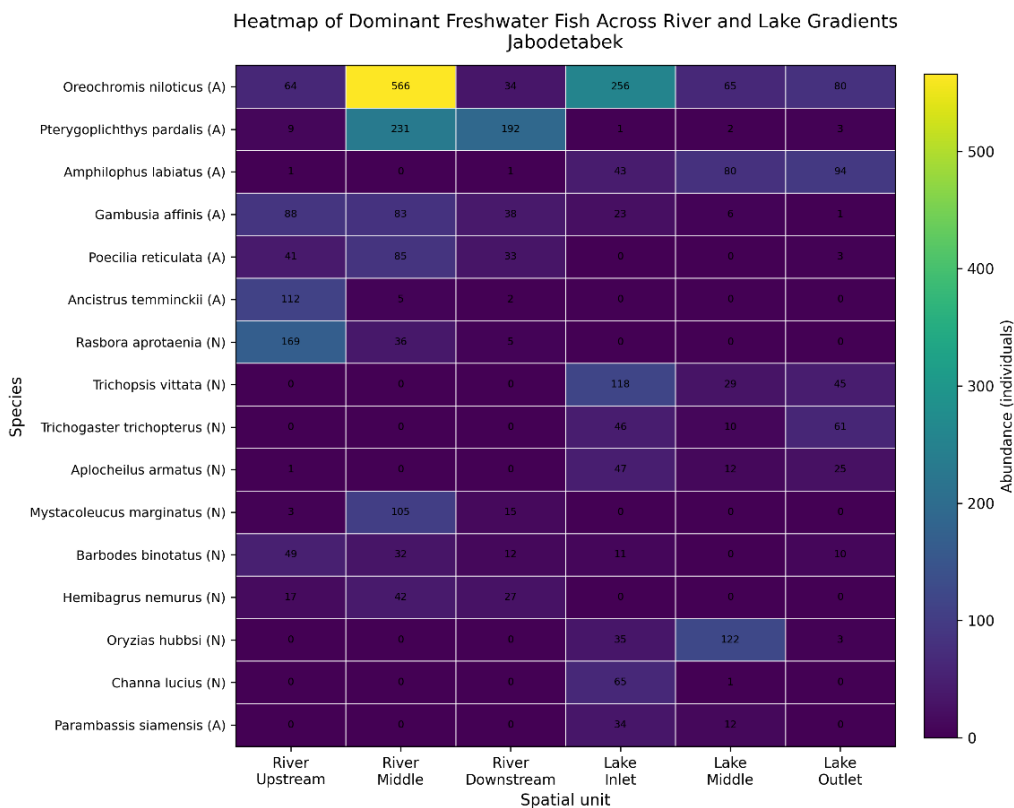


Figure 7. Heatmap of dominant freshwater fish abundance across river and lake spatial gradients in Jabodetabek, Indonesia

Table 13. Integrated synthesis of dominant and ecologically important freshwater fish across river and lake ecosystems in Jabodetabek, Indonesia

Species	Main ecosystem	Total abundance (ind.)	Local distribution (%)	Status	Main spatial pattern	Ecological presentation in manuscript	Inferred contribution to community pattern
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	Rivers and lakes	River: 664; Lake: 411	River: 88.89; Lake: 100	Alien	Concentrated in middle-downstream rivers; abundant in lake inlets and across all lakes	The most widespread alien fish in both ecosystems	Major driver of alien dominance, reduced evenness, and community homogenization
<i>Pterygoplichthys pardalis</i> (Castelnau, 1855)	Rivers > lakes	River: 432; Lake: 6	River: 77.78; Lake: 33.33	Alien	Strong in middle and downstream rivers; minor in lakes	Dominant invasive loricariid, especially in rivers	Strong contributor to river dominance and downstream assemblage simplification
<i>Amphilophus labiatus</i> (Günther, 1864)	Lakes	217	100	Alien	Present across all lake zones	One of the dominant alien cichlids in lakes	An important contributor to lake alien dominance and zonal homogenization
<i>Ancistrus temminckii</i> (Valenciennes, 1840)	Rivers	119	77.78	Alien	Broadly distributed in rivers, especially Cileungsi and Ciliwung	Widespread alien loricariid	Reinforces alien numerical dominance in rivers
<i>Gambusia affinis</i> (Baird & Girard, 1853)	Rivers and lakes	River: 209; Lake: 30	River: 88.89; Lake: 44.44	Alien	Widespread in rivers; lower but present in lakes	Common alien poeciliid	Supports the dominance of disturbance-tolerant assemblages
<i>Poecilia reticulata</i> Peters, 1859	Rivers > lakes	River: 159; Lake: 3	River: 77.78; Lake: 11.11	Alien	Widespread in rivers, rare in lakes	Abundant alien ornamental/livebearer	Adds to river alien dominance and community imbalance
<i>Rasbora aprotaenia</i> Hubbs & Brittan, 1954	Rivers	210	77.78	Native	Strongest in Cileungsi upstream, middle, and present across rivers	Most abundant native river species	Key native indicator within river assemblages despite alien pressure
<i>Mystacoleucus marginatus</i> (Valenciennes, 1842)	Rivers	123	44.44	Native	Concentrated in selected river segments	Abundant native cyprinid	Supports residual native structure in rivers
<i>Barbodes binotatus</i> (Valenciennes, 1842)	Rivers and lakes	River: 93; Lake: 21	River: 77.78; Lake: 33.33	Native	Broad in rivers, localized in lakes	Common native cyprinid	Contributes to native persistence across habitats
<i>Hemibagrus nemurus</i> (Valenciennes, 1840)	Rivers	86	66.67	Native	More frequent in river segments than in lakes	Abundant native bagrid	Represents native predatory/consumptive component in rivers
<i>Trichopsis vittata</i> (Cuvier, 1831)	Lakes	192	100	Native	Present across all lake zones	Dominant native lake species	Important counterbalance to alien dominance in lakes
<i>Trichogaster trichopterus</i> (Pallas, 1770)	Lakes	117	100	Native	Widespread across all lakes and zones	Dominant native anabantiform	Maintains native representation in lake assemblages
<i>Aplocheilichthys armatus</i> (van Hasselt, 1823)	Lakes	90	100	Native	Present across all lake zones	Widespread native species in lakes	Supports native evenness and persistence in lentic habitats
<i>Oryzias hubbsi</i> Roberts, 1998	Lakes	160	44.44	Native	Strongly concentrated in Tonjong and Tunggilis	Numerically abundant but spatially restricted native	Indicates localized native abundance rather than broad dominance
<i>Channa lucius</i> (Cuvier, 1831)	Lakes	66	33.33	Native	Concentrated mainly in Tunggilis	Native predatory fish in lakes	Reflects habitat-specific native retention
<i>Parambassis siamensis</i> (Fowler, 1937)	Lakes	46	44.44	Alien	Present in multiple lake plots but not a dominant system-wide	Alien species with moderate abundance	Secondary contributor to alien component in lakes

Drivers of community change: Water quality and invasive species traits

Environmental gradients, particularly physicochemical water conditions, helped shape fish community change in both riverine and lacustrine habitats. Patterns in Dissolved Oxygen (DO), pH, temperature, and Total Dissolved Solids (TDS) closely matched biological responses across habitats. Similar patterns have been reported in the Ciliwung River, where declining water quality was associated with increasing dominance of tolerant and non-native fishes under urban stress (Mujadid et al. 2025), and similar dynamics occur in urban freshwaters and managed lakes, where degraded water quality, habitat simplification, and nutrient enrichment favor tolerant taxa over sensitive native species (Jeppesen et al. 2005; Walsh et al. 2005). In connected urban river-lake systems, such degradation may spread across habitats through hydrological flow, sediment inputs, and cumulative catchment disturbance. This environmental filtering was reflected in native-alien dominance patterns: Figure 5 shows that alien fishes were substantial in both lakes and rivers, but proportionally higher in rivers, suggesting that invasion success depended not only on propagule presence but also on the compatibility of alien taxa with prevailing habitat conditions. The physicochemical ranges recorded in this study were within the tolerance limits of dominant alien taxa, particularly *O. niloticus* and *P. pardalis*, which can persist under low oxygen, variable temperature, and nutrient-rich conditions (Canonica et al. 2005; Chaichana and Jongphadungkiet 2012). Thus, declining habitat quality not only reduced overall diversity but also restructured assemblages by favoring species able to exploit disturbed conditions, consistent with global evidence that environmental degradation and biological invasion often act together in urban freshwater ecosystems (Rahel 2000; Copp et al. 2005).

Trait-based characteristics further explain this pattern: *O. niloticus* shows high reproductive output, feeding plasticity, and behavioral flexibility, while *Pterygoplichthys* spp. persist in disturbed habitats through benthic feeding, burrowing, and facultative air breathing (Moyle and Marchetti 2006; Nico et al. 2009). Similarly, poeciliids such as *G. affinis* can rapidly colonize disturbed habitats because of their short generation time and broad thermal and salinity tolerance. When these traits interact with physicochemical filtering, community change becomes directional rather than random, favoring a narrower set of tolerant and invasive taxa. Table 4 supports this interpretation by showing that rivers had a larger alien component, lower structural balance, lower Shannon-Wiener Diversity Index, and higher dominance than lakes. Although this analysis is descriptive and does not test causality directly, native-alien dominance (Table 8; Figures 5-6) and ecosystem-level metrics (Table 4) strongly suggest that physicochemical filtering and trait-mediated invasion success influenced fish community change in Jabodetabek freshwater systems.

Management implications

The main management priority is to control *O. niloticus* and *P. pardalis* in invasion hotspots where abundance was highest, and community simplification was most evident. In rivers, priority should focus on the middle and downstream sections of the Cileungsi River, particularly for *O. niloticus* in the middle section and *P. pardalis* in the middle and downstream sections (Table 2). In lakes, *O. niloticus* should be prioritized in the inlet zones of Tunggilis and Suradita, and *A. labiatus* in all lake zones (Table 3). These patterns suggest that management should prioritize invasion hotspots based on diversity, dominance, and native-alien composition rather than applying uniform control across all sites. Site-specific removals using suitable gears may be more effective than broad control because eradication becomes increasingly difficult once invasive populations are established (Hill and Sowards 2015; Orfinger and Gooding 2018). Management in Jabodetabek should prioritize the suppression of reproductive hotspots, reduction of dense local populations, and interruption of introduction pathways, supported by Early Detection and Rapid Response (EDRR) and, where feasible, environmental DNA (eDNA) surveillance (Reaser et al. 2020; Wray et al. 2024). Because these habitats form connected urban river-lake systems, inadequate control in one area may reinforce reinvasion elsewhere. However, invasive fish control alone is unlikely to succeed without improving habitat and water quality. To reduce reinvasion risk and improve conditions for native species, control should be integrated with pollutant reduction, sediment management, riparian buffering, and restoration of channel or shoreline complexity (Oertli and Parris 2019). In rivers, this requires coordinated rehabilitation along the longitudinal continuum, whereas in lakes, management should emphasize shoreline protection, nutrient reduction, and stronger biosecurity against new introductions (Jeppesen et al. 2005; Gozlan et al. 2010). These implications should be interpreted cautiously, given the study's limited temporal coverage and lack of direct causal modeling, but they support the 6R conservation framework for Indonesian biodiversity, which emphasizes integrating invasive-species control with habitat restoration and biodiversity conservation (Hadi et al. 2023). Community-based control may be more feasible for *O. niloticus* because it is widely caught and consumed locally. In contrast, *P. pardalis* is less accepted, although its meal has potential as an alternative feed ingredient (Panase et al. 2018); however, because populations from the Ciliwung River persist in Cd-, Hg-, and Pb-contaminated conditions, contaminant screening is needed before biomass is used in feed chains (Elfidasari et al. 2023). A similar challenge applies to *A. labiatus*, which is less favored for direct consumption, although it may still be processed into products such as fish balls (Ohee and Budi 2021). Accordingly, management should combine selective removals with carefully screened biomass-utilization pathways rather than rely only on market demand or recreational harvest.

In conclusion, across interconnected urban freshwater ecosystems in Jabodetabek, this study revealed clear differences between river and lake fish communities in diversity, invasion pressure, and spatial structure. Rivers supported higher richness and abundance than lakes (38 species, 2,471 individuals vs. 27 species, 1,375 individuals), but also had a larger alien component in both abundance and proportion (1,604 individuals, 64.90% vs. 736 individuals, 50.20%). Although rivers showed slightly higher Shannon-Wiener Diversity Index than lakes ($H' = 1.46$ vs. 1.24), their lower evenness ($E = 0.62$ vs. 0.88) and higher dominance ($C = 0.40$ vs. 0.33) indicated stronger concentration in a few successful taxa. The main alien fishes requiring management attention were *O. niloticus* and *P. pardalis*, with additional concern for *A. temminckii*, *G. affinis*, and *P. reticulata* in rivers, and *A. labiatus* in lakes. The results support the hypothesis that invasive species became more prevalent in degraded downstream river segments, whereas lakes showed lower diversity, higher evenness, and stronger cross-zone homogenization. Management should therefore prioritize selective removal in invasion hotspots, especially downstream river sections and lake inlet zones, while reducing reproductive populations, interrupting introduction pathways, strengthening early detection, and integrating fish control with habitat restoration and lake biosecurity. Overall, rivers retained greater spatial compositional turnover despite localized homogenization in degraded segments, whereas lakes showed broader assemblage convergence across zones. These conclusions should, however, be interpreted cautiously because the study had limited temporal coverage and lacked direct causal modeling, so the observed links among urban disturbance, habitat degradation, and alien fish dominance remain primarily correlational. Future research should move beyond descriptive community patterns by developing a practical framework to assess freshwater habitat vulnerability to alien fish invasion through integrated ecological, physicochemical, habitat, and invasion-related variables, thereby helping identify native refugia, invasion-amplifying habitats, and priority areas for prevention, restoration, and rapid intervention in urban freshwater systems.

ACKNOWLEDGEMENTS

We gratefully acknowledge Yayasan Temali Indonesia Lestari and the Biology Study Program, Universitas Indonesia, Indonesia, for their invaluable support during this research. Their assistance with sampling, logistical support, academic guidance, and commitment to environmental conservation greatly contributed to the successful completion of this study.

REFERENCES

- Albert JS, Destouni G, Duke-Sylvester SM, Magurran AE, Oberdorff T, Reis RE, Winemiller KO, Ripple WJ. 2021. Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* 50 (1): 85-94. <https://doi.org/10.1007/s13280-020-01318-8>.
- Alberti M. 2015. Eco-evolutionary dynamics in an urbanizing planet. *Trend Ecol Evol* 30 (2): 114-126. <https://doi.org/10.1016/j.tree.2014.11.007>.
- Antonelli M, Laube P, Doering M, Scherelis V, Wu S, Humri L, Heitzler M, Weber C. 2024. Identifying anthropogenic legacy in freshwater ecosystems. *Wiley Interdiscip Rev Water* 11 (4): e1729. <https://doi.org/10.1002/wat2.1729>.
- Bonar SA, Mercado-Silva N, Hubert WA, Beard TD, Dave G, Kubečka J, Graeb BDS, Lester NP, Porath M, Winfield IJ. 2017. Standard methods for sampling freshwater fishes: Opportunities for international collaboration. *Fisheries* 42 (3): 150-156. <https://doi.org/10.1080/03632415.2017.1276352>.
- Canonico GC, Arthington A, McCrary JK, Thieme ML. 2005. The effects of introduced tilapias on native biodiversity. *Aquat Conserv Mar Freshw Ecosyst* 15 (5): 463-483. <https://doi.org/10.1002/aqc.699>.
- Chaichana R, Jongphadungkiet S. 2012. Assessment of the invasive catfish *Pterygoplichthys pardalis* (Castelnau, 1855) in Thailand: Ecological impacts and biological control alternatives. *Trop Zool* 25 (4): 173-182. <https://doi.org/10.1080/03946975.2012.738494>.
- Copp GH, Garthwaite R, Gozlan RE. 2005. Risk identification and assessment of non-native freshwater fishes: A summary of concepts and perspectives on protocols for the UK. *J Appl Ichthyol* 21 (4): 371-373. <https://doi.org/10.1111/j.1439-0426.2005.00692.x>.
- Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA. 2006. Freshwater biodiversity: Importance, threats, status, and conservation challenges. *Biol Rev* 81 (2): 163-182. <https://doi.org/10.1017/S1464793105006950>.
- Elfidasari D, Rijal MS, Shalsabilla SE, Rahma Fadila DS, Cici A, Pikoli MR, Tetriana D, Sugoro I. 2023. Intestinal bacteria diversity of suckermouth catfish (*Pterygoplichthys pardalis*) in the Cd, Hg, and Pb contaminated Ciliwung River, Indonesia. *Heliyon* 9 (4): e14842. <https://doi.org/10.1016/j.heliyon.2023.e14842>.
- Elfidasari D, Wijayanti F, Muthmainah HF. 2020. Habitat characteristics of suckermouth armored catfish *Pterygoplichthys pardalis* in Ciliwung River, Indonesia. *Intl J Fish Aquat Stud* 8 (3): 141-147.
- Gozlan RE, Britton JR, Cowx I, Copp GH. 2010. Current knowledge on non-native freshwater fish introductions. *J Fish Biol* 76 (4): 751-786. <https://doi.org/10.1111/j.1095-8649.2010.02566.x>.
- Grill G, Lehner B, Thieme M, Geenen B, Tickner D, Antonelli F, Babu S, Borrelli P, Cheng L, Crochetiere H, Ehalt MH. 2019. Mapping the world's free-flowing rivers. *Nature* 569 (7755): 215-221. <https://doi.org/10.1038/s41586-019-1111-9>.
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008. Global change and the ecology of cities. *Science* 319 (5864): 756-760. <https://doi.org/10.1126/science.1150195>.
- Hadi N, Ainy NS, Sjahfirdi L, Mujadid I. 2023. The 6R principles of biodiversity conservation and protection: Arresting the rate of extinction and major threats to wildlife in Indonesia. *Jurnal Green Growth dan Manajemen Lingkungan* 13 (1): 44-61. <https://doi.org/10.21009/10.21009.134>.
- Hadiaty RK. 2011. Diversitas dan hilangnya jenis-jenis ikan di Sungai Ciliwung dan Sungai Cisadane. *Berita Biologi* 10 (4): 491-504. [Indonesian]
- Havel JE, Kovalenko KE, Thomaz SM, Amalfitano S, Kats LB. 2015. Aquatic invasive species: Challenges for the future. *Hydrobiologia* 750 (1): 147-170. <https://doi.org/10.1007/s10750-014-2166-0>.
- Hill JE, Sowards J. 2015. Successful eradication of the non-native loricariid catfish *Pterygoplichthys disjunctivus* from the Rainbow River, Florida. *Manag Biol Invasion* 6 (3): 311-317. <https://doi.org/10.3391/mbi.2015.6.3.11>.
- Jeppesen E, Sondergaard M, Jensen JP, Havens KE, Anneville O, Carvalho L, Coveney MF, Deneke R, Dokulil MT, Foy BO, Gerdeaux D. 2005. Lake responses to reduced nutrient loading - An analysis of contemporary long-term data from 35 case studies. *Freshw Biol* 50 (10): 1747-1771. <https://doi.org/10.1111/j.1365-2427.2005.01415.x>.
- Kottelat M, Whitten T. 1996. *Freshwater Biodiversity in Asia with Special Reference to Fish*. World Bank Publications. Washington DC. <https://doi.org/10.1596/0-8213-3808-0>.
- Lawson L, Edge CB, Fortin MJ, Jackson DA. 2024. Temporal change in urban fish biodiversity-Gains, losses, and drivers of change. *Ecol Evol* 14 (2): e10845. <https://doi.org/10.1002/ece3.10845>.
- Lokatis S, Jeschke JM. 2022. Urban biotic homogenization: Approaches and knowledge gaps. *Ecol Appl* 32 (8): e2703. <https://doi.org/10.1002/eap.2703>.

- McDonnell MJ, Hahs AK. 2015. Adaptation and adaptedness of organisms to urban environments. *Annu Rev Ecol Evol Syst* 46: 261-280. <https://doi.org/10.1146/annurev-ecolsys-112414-054258>.
- Moyle PB, Marchetti MP. 2006. Predicting invasion success: Freshwater fishes in California as a model. *BioScience* 56 (6): 515-524. [https://doi.org/10.1641/0006-3568\(2006\)56\[515:PISFFI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[515:PISFFI]2.0.CO;2).
- Mujadid I, Ainy N. 2025. 14 Alien Fish Jabodetabek. *Zenodo* 1 (1): 1-39. <https://doi.org/10.5281/zenodo.17747888>.
- Mujadid I, Ainy NS, Hadi N. 2025. Reinventarisasi dan analisis laju peningkatan diversitas ikan di Sungai Ciliwung. *Berita Biologi* 24 (2): 279-296. https://doi.org/10.55981/berita_biologi.2025.4921. [Indonesian]
- Nico LG, Jelks HL, Tuten T. 2009. Non-native suckermouth armored catfishes in Florida: Description of nest burrows and burrow colonies with assessment of shoreline conditions. *Aquat Nuisanc Spec Res Progr Bull* 9 (1): 1-30.
- Nuryanto A, Bhagawati D, Abulias MN, Indarmawan. 2015. Fauna ikan di Sungai Cikawung, Kabupaten Cilacap, Jawa Tengah. *J Iktiologi Indones* 15 (1): 25-37. <https://doi.org/10.32491/jii.v15i1.73>. [Indonesian]
- Nuryanto A, Bhagawati D, Nadjmi AM, Indarmawan. 2016. Ichthyofauna at Cijalu River, Cilacap regency, Central Java Province, Indonesia. *Biotropia* 23 (1): 1-9. <https://doi.org/10.11598/btb.2016.23.1.362>.
- Oertli B, Parris KM. 2019. Review: Toward management of urban ponds for freshwater biodiversity. *Ecosphere* 10 (7): e02810. <https://doi.org/10.1002/ecs2.2810>.
- Ohee HL, Budi IM. 2021. Pemanfaatan ikan Red Devil cichlid (*Amphilophus labiatus*, Günther 1864) dari Danau Sentani, Jayapura, Papua. *J Pengabdian Papua* 5 (1): 1-7. <https://doi.org/10.31957/jpp.v5i1.1586>. [Indonesian]
- Olden JD. 2006. Biotic homogenization: A new research agenda for conservation biogeography. *J Biogeogr* 33 (12): 2027-2039. <https://doi.org/10.1111/j.1365-2699.2006.01572.x>.
- Orfinger AB, Goodding DD. 2018. The global invasion of the suckermouth armored catfish genus *Pterygoplichthys* (Siluriformes: Loricariidae): Annotated list of species, distributional summary, and assessment of impacts. *Zool Stud* 57: 7. <https://doi.org/10.6620/ZS.2018.57-07>.
- Panase P, Uppapong S, Tuncharoen S, Tanitson J, Soontornprasit K, Intawicha P. 2018. Partial replacement of commercial fish meal with Amazon sailfin catfish *Pterygoplichthys pardalis* meal in diets for juvenile Mekong giant catfish *Pangasianodon gigas*. *Aquac Rep* 12: 25-29. <https://doi.org/10.1016/j.aqrep.2018.08.005>.
- Rahel FJ, Olden JD. 2008. Assessing the effects of climate change on aquatic invasive species. *Conserv Biol* 22 (3): 521-533. <https://doi.org/10.1111/j.1523-1739.2008.00950.x>.
- Rahel FJ. 2000. Homogenization of fish faunas across the United States. *Science* 288 (5467): 854-856. <https://doi.org/10.1126/science.288.5467.854>.
- Reaser JK, Burgiel SW, Kirkey J, Brantley KA, Veatch SD, Burgos-Rodríguez J. 2020. The early detection of and rapid response (EDRR) to invasive species: A conceptual framework and federal capacities assessment. *Biol Invasion* 22 (1): 1-19. <https://doi.org/10.1007/s10530-019-02156-w>.
- Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol Rev* 94 (3): 849-873. <https://doi.org/10.1111/brv.12480>.
- Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can* 191: 1-382.
- Sarifah AN, Mujadid I, Hadi N, Sjahfirdi L. 2024. Increase in the abundance of invasive fish species in the Ciliwung River, DKI Jakarta, and West Java Provinces. *ADI J Recent Innov* 6 (1): 17-31. <https://doi.org/10.34306/ajri.v6i1.1060>.
- Strayer DL, Dudgeon D. 2010. Freshwater biodiversity conservation: Recent progress and future challenges. *J N Am Benthol Soc* 29 (1): 344-358. <https://doi.org/10.1899/08-171.1>.
- Suryaningsih S, Sukmaningrum S, Simanjuntak SBI, Kusbiyanto. 2017. Diversity and longitudinal distribution of freshwater fish in Klawing River, Central Java, Indonesia. *Biodiversitas* 19 (1): 85-92. <https://doi.org/10.13057/biodiv/d190114>.
- Tickner D, Opperman JJ, Abell R, Acreman M, Arthington AH, Bunn SE, Cooke SJ, Dalton J, Darwall W, Edwards G, Harrison I. 2020. Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *BioScience* 70 (4): 330-342. <https://doi.org/10.1093/biosci/biaa002>.
- Vörösmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S, Bunn SE, Sullivan CA, Liermann CR, Davies PM. 2010. Global threats to human water security and river biodiversity. *Nature* 467 (7315): 555-561. <https://doi.org/10.1038/nature09440>.
- Walsh CJ, Roy AH, Feminella JW, Cottingham PD, Groffman PM, Morgan RP. 2005. The urban stream syndrome: Current knowledge and the search for a cure. *J N Am Benthol Soc* 24 (3): 706-723. <https://doi.org/10.1899/04-028.1>.
- Wei H, Copp GH, Vilizzi L, Liu F, Gu D, Luo D, Xu M, Mu X, Hu Y. 2017. The distribution, establishment, and life-history traits of non-native sailfin catfishes, *Pterygoplichthys* spp. In the Guangdong province of China. *Aquat Invasion* 12 (2): 241-249. <https://doi.org/10.3391/ai.2017.12.2.11>.
- Wray AK, Agnew AC, Brown ME, Dean EM, Hernandez ND, Jordon A, Moringstar CR, Piccolomini SE, Pickett HA, Daniel WM, Reichert BE. 2024. Understanding gaps in early detection of and rapid response to invasive species in the United States: A literature review and bibliometric analysis. *Ecol Inform* 84: 102855. <https://doi.org/10.1016/j.ecoinf.2024.102855>.
- Zengeya TA, Booth AJ, Chimimba CT. 2015. Broad niche overlap between invasive Nile tilapia *Oreochromis niloticus* and indigenous congeners in Southern Africa: Should we be concerned? *Entropy* 17 (7): 4959-4973. <https://doi.org/10.3390/e17074959>.