frontiers | Frontiers in Environmental Science

TYPE Original Research
PUBLISHED 15 September 2022
DOI 10.3389/fenvs.2022.943586

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Freshwater Science,
a section of the journal
Frontiers in Environmental Science

RECEIVED 13 May 2022
ACCEPTED 03 August 2022
PUBLISHED 15 September 2022

CITATION
Moraga D, Vivancos A, Ruiz VH, Rojas O, Díaz G, Manosalva A, Vega P and Habit E (2022), A century of anthropogenic river alterations in a highly diverse river coastal basin: Effects on fish assemblages.
Front. Environ. Sci. 10:943586.
doi: 10.3389/fenvs.2022.943586

A century of anthropogenic river alterations in a highly diverse river coastal basin: Effects on fish assemblages

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The global increase in human population is driving a continuous conversion of land to anthropogenic uses. This is a major threat to lotic ecosystems worldwide, as it compromises the biotic integrity and health of rivers and streams. Studies in the northern hemisphere have shown that the effects of urbanization on fish assemblages include decrease and/or loss of diversity and abundance of native species, and a proliferation of tolerant exotic species. Such effects have not been widely studied in developing countries like Chile, where urbanization has impacted several river ecosystems. Over decades, the lower zone of the Andalién River in Central Chile has gone over intense non-planned urbanization stemming from the city of Concepción, leading to several physical alterations. The native fish and lamprey fauna of this coastal river basin has been reported as very diverse, with a total of 16 native species. However, this fauna has been affected by multiple effects of different land uses and direct alterations in the riverbed. To study how these fish and lamprey assemblages have changed, this paper compiles records from 1919 to 2018 and analyzes them in relation to the direct and indirect anthropogenic alterations in the basin. The results show a significant reduction in richness and abundance of native species, with only nine species currently. The two migratory lampreys, one of them endemic (*Mordacia lapicida*), have been extirpated from the Andalién River basin. Conversely, the richness and distribution of introduced species has increased throughout the river basin. The invasive species *Gambusia holbrooki*, first registered in 1999, is currently the most abundant in the urban zone of the river. Although the more substantial direct alterations of the riverbed occurred in the lower areas, a steeper reduction in native species richness occurred in the middle areas subjected to a long history of agricultural and forestry land use. We suggest the loss of resilience of the river ecosystem, and that the collapse of biodiversity in this river system demonstrates the lack of urban planning and the inefficiency of environmental regulations in protecting native species and ecosystems with high conservation value in Chile.

KEYWORDS
Andalién River, land use, urbanization, channelization, river resilience, native fish, Chile

Introduction

Land use conversion is a pervasive threat to freshwater ecosystems that impacts water quality, increases water temperature, and alters hydrologic regimes and physical habitats (Chen and Olden, 2020). The conversion of natural habitats to agricultural, forest or urban uses not only affects terrestrial ecosystems but also substantially influences the biodiversity and biological integrity of streams and rivers flowing through these landscapes (Walters et al., 2009; Tóth et al., 2019). At the catchment scale, studies have reported threshold values ranging up to 50% agricultural land use and 5%–25% urban land use. When thresholds were exceeded, fundamental shifts in fish assemblage structure were observed (Chen and Olden, 2020). The hydrological and morphological alterations due to urbanization have been summarized as the so-called 'urban stream syndrome' (Walsh et al., 2005; Bierschenk et al., 2019). This model predicts a loss of sensitive native fish species, while tolerant fish species, mostly exotic, increase (Walsh et al., 2005; Engman and Ramírez, 2012).

Channelization and urbanization are anthropogenic alterations that act on the reach and catchment scale, respectively, degrading stream habitats (Engman and Ramírez, 2012). In urban areas, streams are often confined in channels covered with impervious concrete surfaces. Combined with the alteration of the riparian zone, these modifications result in channel simplification and homogenized habitat structure (Czeglédi et al., 2020). These effects cause important environmental deterioration, which strongly influences biodiversity (Gál et al., 2019; Tóth et al., 2019), for example, altering trophic food webs and triggering the loss of aquatic species (Fierro et al., 2019). Within catchments, the lowlands or potamon zones of rivers are the most impacted, as they accumulate the effect of anthropogenic activities throughout the river basin (McCluney et al., 2014; Jenkins, 2018; Arriagada et al., 2019). In urban streams, typical responses on fish fauna are decreased assemblage diversity and evenness (Rieck and Sullivan, 2020), and increased assemblages' homogenization (Marchetti et al., 2006; Walters et al., 2009).

Understanding how, and over what time scales, land use changes and urbanization alter ecological characteristics, is a critical step in further understanding and effectively managing urban streams (Rieck and Sullivan, 2020). This is particularly true in developing countries such as Chile, where the magnitude of anthropogenic pressures, coupled with weak environmental regulation and management, threaten sustainability (Habit et al., 2019). In the potamon zones of Chilean rivers, urbanization is the biggest cause of river ecosystem alterations (Fierro et al., 2019). In contrast, potamon zones host the highest abundance and species richness of native Chilean fish and lampreys (Habit et al., 2006).

In central Chile, the small coastal basin of the Andalién River is characterized by a high diversity of native fish and lampreys. Despite its high conservation value, the lower zone of the Andalién River has become part of the country's second-biggest metropolitan area, the city of Concepción. As such, numerous productive activities have been developed, causing several impacts on the river ecosystem (Jaque, 1996; Habit et al., 2007). The upper and middle zones of the river basin initially experienced a strong agricultural development, followed by extensive forestry plantation with exotic species over the last 40 years (General Directorate of Water, 2004). Furthermore, due to non-planned urban development, the floodplain of the lower zone of the Andalién River has been populated, increasing the number and magnitude of urban flood events (Rojas et al., 2017). This situation has led to the dredging and channelization of the river and lower tributaries to mitigate these events. Such anthropogenic river alterations have direct and indirect effects on the aquatic ecosystem, like alteration of the flow regime, fluvial geomorphology, and water quality (González del Tánago and García de Jalón, 1998; Pauchard et al., 2006; Aguayo et al., 2009).

The aim of this study was to determine how direct and indirect changes to rivers and streams of a coastal basin under non-planning development, have impacted fish and lamprey assemblages throughout 100 years of anthropogenic alterations. Long-term data on fish presence and abundance were analyzed in relation to different anthropogenic river alterations. Additionally, to detect the impact of flood mitigation actions on fish and lamprey richness, a Before-After-Control-Impact model was performed. This approach applies to other urban river ecosystems and advances in the understanding of how these alterations can affect freshwater species and river ecosystem resilience.

Materials and methods

Study area

The Andalién River basin is located in the Biobío region of Chile and originates in the coastal range (Cordillera de la Costa) in the south of the Chilean Mediterranean climate zone (36°45S, 72°50′W). It covers a drainage area of 775 km^2 and the main channel length is 36 km (Figure 1; General Directorate of Water, 2004; Arriagada et al., 2019). The flow regime is pluvial with winter rains. Average annual flow is 12.5 ± 6.6 m^3/s with maximum thresholds of 572 m^3/s [statistics of 40 years; Center for Climate and Resilience Research $(CR)^2$]. Currently, the native

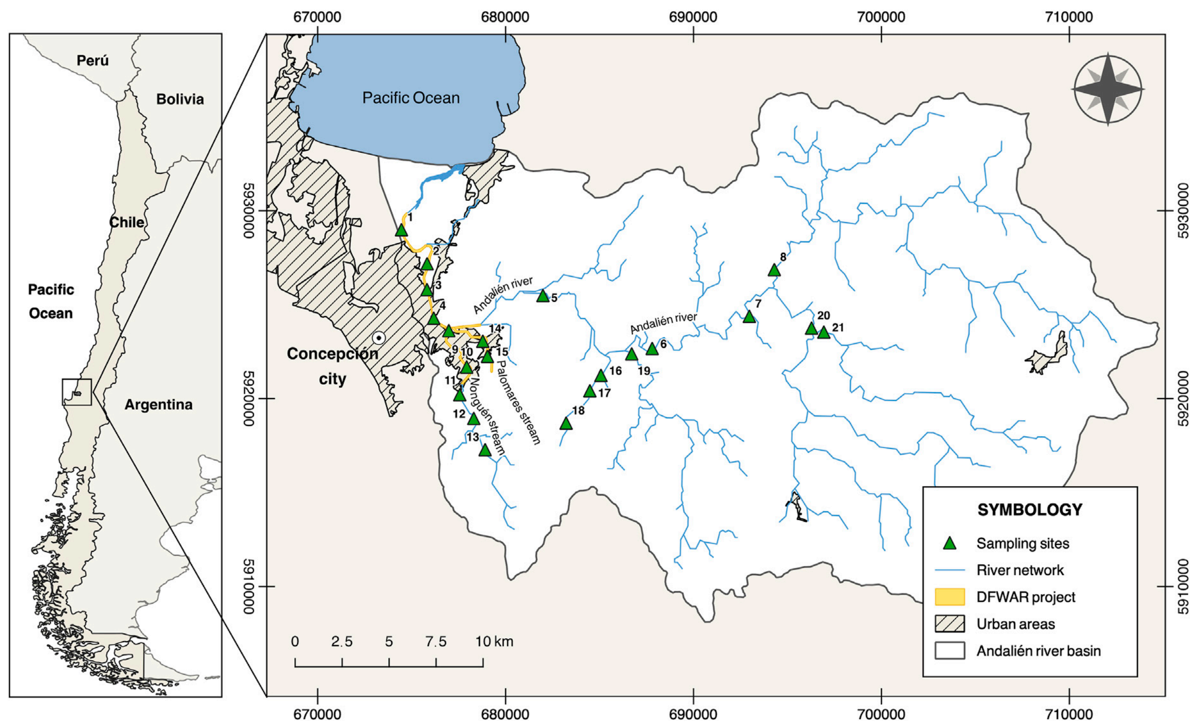

FIGURE 1
Andalién River basin and locations of all sampling sites with fish data. The channelization zone is shown in yellow.

forest covers 16.1% of the basin area. Predominant land uses correspond to forest plantations (54.5%), scrublands (11.9%), agriculture (10.6%), and urban areas (3.5%) (National Forest Corporation, 2015). Urban land use is concentrated in the lower area of the basin, which is home to 171,364 inhabitants, equivalent to 97% of the total population of the basin (National Institute of Statistics, 2017).

The urban population is distributed along the riverbanks of the Andalién River and its lower tributary, the Nonguén stream. Between 1943 and 2011, the city of Concepción grew 14.5 km^2 directly on the floodplain of the Andalién River (Mardones et al., 2004; Vidal and Romero, 2010; Rojas et al., 2017). In fact, 65.3% of the urban growth occurred in geomorphological areas susceptible to flooding (Rojas et al., 2017). Consequently, 21 flood events have been registered in populated areas between 1960 and 2010 (Rojas et al., 2017). In 2006 the river reached the maximum flow of 572 m^3/s (Rojas et al., 2018), causing the most significant flood event. In response, government agencies executed works such as dredging, rectifications, and ducts along the Andalién River, lower tributaries (Nonguén and Palomares streams) and the estuary (Rojas et al., 2019). Although these actions were approved through the Environmental Impact Assessment System (SEIA) (DS 40/2013 of the Ministry of the Environment), multiple impacts of river alterations were not considered. Therefore, the high conservation value of the fish and lamprey fauna of the Andalién River (Ruiz, 1993; Habit et al., 2007) was not well assessed.

Analysis of temporal changes in the basin

Anthropogenic alterations with potential impacts on the fish and lamprey assemblages were analyzed. Direct alterations on the riverbed along the river basin were evaluated by analyzing the environmental impact assessment of approved projects from 1997 to 2017. Each project was classified according to its typology (Art. 3 of DS.95/1997 and DS. 40/2013), and activities that generated direct physical changes in the riverbed were recognized (*e.g.,* dredging, channelization, cofferdams for bridge-building). Indirect alterations were evaluated through changes in both land use and land cover area (classified as urban, agricultural, and forestry use), using available information from 1996 to 2015, provided by the National Forest Corporation (National Forest Corporation, 1996; National Forest Corporation, 2015)

Data collection

Data on presence and abundance of fish and lamprey species were obtained from three sources: scientific studies, technical reports, and samplings carried out for this research (Supplementary Table S1). Existent scientific publications are Oliver (1949), who reported samples from 1919 in two sites in the Andalién River and the Nonguén stream (Figure 1); Ruiz (1993), who sampled 12 sites in the Andalién River and the Nonguén, Chaimavida, Curapalihue, Poñen, Paso Ancho and Cangrejillo streams in 1986; Habit et al. (2003) who sampled five sites along the Nonguén stream in 1999 and 2000; Habit et al. (2007) with nine sample sites in 2004 in the Andalién River and the Nonguén and Queule streams; and Ortiz-Sandoval et al. (2009), who provided sampling data from 2006 to 2007 from the Andalién River and Nonguén stream. The only data provided by technical reports were associated with the environmentally approved project "Design of fluvial works in the Andalién, Nonguén, and Palomares rivers" (DFWAR). This project comprises the dredging and widening of the middle and lower zones of the Andalién River along 10.1 km. In addition, it includes the rectification and channelization of two lower tributaries (2.0 km along the Nonguén stream and 2.7 km along the Palomares stream; Figure 1). It started in 2006 and is still in progress. According to its environmental permit (RCA N°267/2008) DFWAR executes a monitoring program of fish assemblages. Technical reports contain results of fish samples from 2010 onwards in the Andalién River and the Nonguén and Palomares streams.

Finally, to know the current situation of the fish and lamprey assemblages, samplings were carried out in April 2017 and January 2018 at 14 sampling sites along the Andalién River and the Nonguén, Queule, Chaimavida, Curapalihue, and Poñen streams (Figure 1). At each sampling site, three people conducted fish sampling using a Halltech HT-2000 backpack electrofisher during 20–30 min depending on the available habitat area. Also, fish were captured using beach seines (5 m long, 1.5 m high and 10 mm stretched mesh size) in shallow water habitats (<1 m depth), characterized by gravel, and sand patches. Specimens collected were anesthetized and identified to species level, according to specialized identification keys (Dyer, 2000; Ruiz and Marchant, 2004; Salas et al., 2012), counted, and returned to their habitats. Fish sampling and handling was performed following bioethical protocols established by Chilean Fisheries Subsecretary (SUBPESCA) and the Bioethical Committee of the University of Concepción, Chile.

Data analysis

Analyses were performed to determine temporal changes in the composition and assemblage structure based on presence-absence (1919–2018) and relative abundance data (1986–2018). Sampling sites were grouped according to their position within the river network in: 1) rithron, or headwaters, characterized by cold water temperature (<12°C during summer), high current velocity (>0.3 m/s) and substratum of boulders (>10 cm diameter), 2) transition between rithron and potamon, and 3) potamon, or lower areas, characterized by high water temperature (>12°C in summer), low velocity (<0.3 m/s) and fine substratum (sand or mud) (*sensu* Habit et al., 2007). Analyses were performed at the basin scale, considering these three ecological zones. In addition, effects on fish assemblages due to direct alterations within the urban area were analyzed in the Andalién River and Nonguén stream.

A non-metric multidimensional scaling analysis (nMDS) was carried out to explore changes in fish assemblage structure over time, overlaying a time trajectory from 1986 to 2018. The nMDS was based on a Bray-Curtis dissimilarity matrix, using the annual average of the fish relative abundance, previously standardized and fourth root transformed. A similarity analysis (ANOSIM) was performed to determine statistical effects of dredging and river channelization on fish assemblage structure, comparing pre- and post-alteration periods. This analysis compares dissimilarity between and within time periods. Furthermore, a similarity percentage analysis (SIMPER) was used to know fish species' contribution to each period. PRIMER-E v7.0 program (Clarke and Gorley, 2015) was used for data treatment and analysis. For these analyses that consider relative abundance data, as different sources of fish data were used, it was decided to use the sum of the specimens captured at each site for the samplings carried out for this research, that is, the sum of the specimens captured with the electrofishing backpack and the three seining events.

Additionally, to understand impacts of the DFWAR project on the fish species richness, a Before-After-Control-Impact (BACI) model was designed (Green, 1979). For the study design, the homogeneity between the sampled sites was used to determine control areas in relation to impacted areas, while 2006 was taken as the starting point ("before and after"; Figure 2). This kind of design relies on samples with pseudo-replication issues, as sampling is repeated across sites and pooled across period (before and after disturbances). To account for these issues, we used a GLMM (General Linear Mixed model), where the response variable (i.e., species richness) is modeled with a Poisson distribution, treatment (i.e., Control or Impact) is a fixed effect, while sampling location and sampling period are random effects. Following approach detailed in Pardini et al. (2018), we used parametric bootstrap method to test for statistical significance of the BACI effect using the *"pbkrtest"* package (Halekoh and Højsgaard, 2014). We used the function "lsmeans" from the package *"lsmeans"* (Lenth, 2016) to compute least square means value for species richness before and after the project, in control and impacted sites. Analyses were performed using the "glmer" function in the *"lme4"* package (Bates et al., 2015) in the statistical program R (R Core Team, 2017).

Results

Temporal analysis of anthropogenic activities in the basin

From 1997 to 2017, 37 projects were environmentally approved within the Andalién River basin, and 89% were

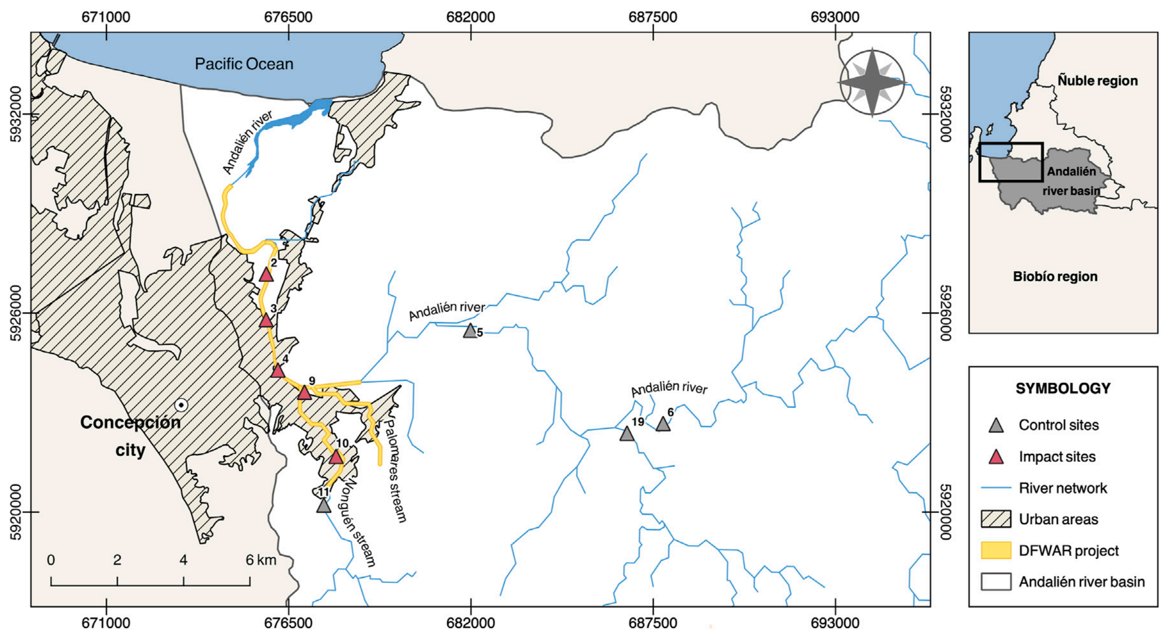

FIGURE 2
Sampling sites used for the BACI analysis in the study area.

assessed through an Environmental Impact Study. The most frequent projects related to real estate (32%), sanitation (22%), equipment (19%), mining (11%), hydraulic infrastructure (8%), transport infrastructure (5%) and energy (3%). Of all projects, 87% were carried out in the lower area of the basin and 78% were directly related to the growth of Concepción city. Of the total, 14% directly modified the riverbed of some river system, corresponding mainly to transport infrastructure projects [Penco-Talcahuano Interport Route (2004); Concepción-Cabrero Highway, (2011)] and hydraulic infrastructure. The latter corresponded to works to mitigate the risks of flooding and for drinking water supply. The DFWAR project has significantly changed the river geomorphology of the Andalién River potamon zone, impacting 6% of the total length of the river network. This project began in 2006, with the dredging, widening and rectification of the lower zone of the Andalién riverbed. Works started 1.3 km upstream of the confluence with the Nonguén stream and up to 2.7 km upstream of its outlet, completing a total 10.1 km of alterations (Figure 3). Dredging, rectification, and subsequent channelization of the potamon zones of the lower tributaries, Nonguén and Palomares streams, occurred during 2010 and 2011. The last 2 km of the 9.2 km long Nonguén stream were channelized with concrete coating. The Palomares stream was channelized and piped for 2.7 km (40% of its total length). The DFWAR project includes waterworks every year before the high flow season.

Changes in land use in the basin between 1996 and 2017 show an 11.3% decrease in land for agricultural use, but an increase in forest plantations (3.5%) and urban areas (1.2%) (Supplementary Figure S1). The length of the river network decreased by 4% between 1978–2011, due to the elimination of meanders and channel rectifications. The bankfull area increased by 28.5% at the Andalién River and 56% at the Nonguén stream because of dredging and channel expansion processes (Rojas et al., 2017).

Temporal patterns of fish composition

Fish data were obtained for 21 sampling sites, between 1919 and 2018. Of the 21 sites, eight were located in rithron zone, eight in transition zone, and five in potamon zone. Between 1919 and 2018, 22 fish species—16 native and six introduced - were reported for the Andalién River basin. The comparison of historical records by river zones (rithron, transition, potamon) with the 2017/18 samples revealed that seven native species were not captured later on: *Geotria australis* (last record in 2015), *Mordacia lapicida* (2013), *Trichomycterus chiltoni* (2004), *Odontesthes mauleanum* (2007), *Percichthys melanops* (2004), and *Percilia gillissi* (2011) (Table 1). In addition, *Nematogenys inermis, Bullockia maldonadoi, Trichomycterus areolatus, Galaxias maculatus, Brachygalaxias bullocki* and *Percilia irwini* have been lost or became very rare in at least one of the three river

FIGURE 3
Potamon area of the Nonguén stream. **(A)** 2004, pre-channeling; **(B)** 2018, post-channeling, Potamon area of the Andalién River; **(C)** 2006 during dredging work in the riverbed; **(D)** 2018, post-widening and deepening of the channel.

zones (Table 1). The only native species that maintain their distribution are *Cheirodon galusdae, Perchithys trucha* and *Basilichthys microlepidotus*. Yet, none of the introduced species has disappeared from the basin, and one has increased its presence (Table 1). According to 1919 records, *Cyprinus carpio* was the only non-native species in the basin. The salmonids *Onchorhynchus mykiss* and *Salmo trutta* first appeared in 1986 records and *Gambusia holbrooki* in 1999. Finally, *Carassius carassius* and *Australoheros facetus* were registered for the first time in 2004.

Comparing the records from 1919 with current surveys in the potamon areas of the Andalién River and the Nonguén stream, it can be noted that the richness of native species has been reduced by 60% (loss of six species) in the dredged area of the Andalién River and by 81% (loss of nine species) in the channelized section of the Nonguén stream (Table 2). Whereas, the richness of introduced species has increased by 300% in the Andalién River and 100% in the Nonguén stream. Furthermore, the exotic species *G. holbrooki* is currently present in both Andalién and Nonguén potamal zone.

Fish assemblage structure analysis

The time trajectory of fish assemblage structure in the Andalién River basin showed gradual assemblage changes during the first consecutive years of sampling (1986–1999-2000–2002-2004–2006). Coincidently with the beginning of the dredging activities, fish assemblage structure substantially changed from 2007 to 2010, 2010 to 2011, and 2011 to 2012, showing, increased dissimilarity and dispersion among years (Figure 4).

The fish assemblages' structure in the Andalién River's potamon area showed significant differences between periods of pre-alteration (1986–2005) and post-alteration (2006–2018) in the riverbed ($R_{Andalién} = 0.283$, $p = 0.001$). Changes are explained by an increase in the abundance of *C. galusdae, G. maculatus* and *G. holbrooki*, and the loss of *M. lapicida*, *G. australis, P. irwini* and *A. facetus* (Table 3). The fish assemblage of the potamon area of Nonguén stream also showed significant differences between the two periods ($R_{Nonguén} = 0.141$ and $p = 0.001$). However, unlike in the Andalién River, the differences resulted from the abundance reduction of all species (Table 4).

TABLE 1 Historical records of species in the Andalién River basin. Their origin (native or introduced), endemism to Chile, conservation status according to the Ministry of the Environment's species classification regulation, and presence in the basin, which are indicated and compared with all records collected during the 2017–2018 samplings by river zones.

Family	Species	Native	Endemism	Conservation category	Past/Current presence		
					Rithron	Transition	Potamon
Geotridae	*Geotria australis* (Gray, 1851)	Yes	No	Vulnerable	Yes/No	Yes/No	Yes/No
Mordaciidae	*Mordacia lapicida* (Gray, 1851)	Yes	Yes	Endangered	No/No	Yes/No	Yes/No
Characidae	*Cheirodon galusdae* (Eigenmann, 1928)	Yes	Yes	Vulnerable	Yes/Yes	Yes/Yes	Yes/Yes
Trichomycteridae	*Nematogenis inermis* (Guichenot, 1848)	Yes	Yes	Endangered	Yes/Yes	Yes/Yes	Yes/No
	Bullockia maldonadoi (Eigenmann, 1928)	Yes	Yes	Endangered	Yes/Yes	Yes/Yes	Yes/No
	Trichomycterus aerolatus (Valenciennes, 1848)	Yes	No	Vulnerable	Yes/Yes	Yes/Yes	Yes/No
	Trichomycterus chiltoni (Eigenmann, 1927)	Yes	Yes	Endangered	Yes/No	Yes/No	Yes/No
Galaxiidae	*Galaxias maculatus* (Jenyns, 1842)	Yes	No	Vulnerable	No/No	Yes/No	Yes/Yes
	Brachygalaxias bullocki (Regan, 1908)	Yes	Yes	Vulnerable	Yes/No	Yes/Yes	Yes/No
Atherinopsidae	*Basilichthys microlepidotus* (Jenyns, 1841)	Yes	Yes	Vulnerable	Yes/Yes	Yes/Yes	Yes/Yes
	Odontesthes mauleanum (Steindachner, 1896)	Yes	Yes	Vulnerable	No/No	Yes/No	Yes/No
Percichthyidae	*Percichthys trucha* (Valenciennes, 1833)	Yes	No	Almost endangered	Yes/Yes	Yes/Yes	Yes/Yes
	Percichthys melanops (Girard, 1855)	Yes	Yes	Vulnerable	Yes/No	Yes/No	Yes/No
Perciliidae	*Percilia irwini* (Eigenmann, 1927)	Yes	Yes	Endangered	Yes/Yes	Yes/Yes	Yes/No
	Percilia gillisi (Girard, 1863)	Yes	Yes	Endangered	Yes/No	Yes/No	Yes/No
Mugilidae	*Mugil cephalus* Linnaeus, 1758	Yes	No	-	No/No	No/No	Yes/No
Salmonidae	*Oncorhynchus mykiss* (Walbaum, 1792)	No	-	-	Yes/Yes	Yes/Yes	Yes/No
	Salmo trutta (Linnaeus, 1758)	No	-	-	Yes/Yes	Yes/Yes	Yes/Yes
Cyprinidae	*Cyprinus carpio* (Linnaeus, 1758)	No	-	-	No/No	No/No	Yes/Yes
	Carassius carassius (Linnaeus, 1758)	No	-	-	No/No	No/Yes	Yes/No
Poecilidae	*Gambusia holbrooki* (Girard, 1859)	No	-	-	No/No	Yes/Yes	Yes/Yes
Cichlidae	*Australoheros facetus* (Jenyns, 1842)	No	-	-	No/No	Yes/Yes	Yes/No

Impact of fluvial works in the Andalién River basin on fish richness

The chosen GLMM only included year as random effect, as site location had very limited contribution in the model. There was a significant BACI period x treatment effect (PBtest = 6.0052, $p = 0.025$). Species richness decreased significantly between the period before and after impact (Figure 5). The estimated mean species richness in impacted sites dropped from 3.53 to 2.07, while in control sites, it dropped from 5.26 to 3.08 and looking at the difference between the change of species richness in both treatments, we found that control sites had a steeper loss of species richness (−0.72) (cf. Table 5 and Figure 6).

Discussion

Here we have documented a dramatic example of how the combination of lacking urban planning, with weak environmental regulations, has caused the collapse of a highly valuable fish and lamprey fauna. Although the more substantial direct alterations of the riverbed occurred in the lower areas, a steeper reduction in native species richness occurred in the middle areas subjected to a long history of agricultural and forestry land use. These severe changes in fish assemblages and its habitat suggest the loss of resilience of the river ecosystem, probably with significant modifications in productivity, connectivity, and environmental heterogeneity (Van Looy et al., 2019).

Coastal river basins and lower zones of large rivers exhibit important urban settlements and land use changes due to the virtuous combination of proximity to marine coastal zones and freshwater provision. In Chile, rivers originating in the Coastal Mountain range present smaller areas and shorter extensions, than the Andean rivers. However, the coastal river basins exhibit a disproportionately high native fish species richness (Habit and Victoriano, 2005). For example, the highest native species richness in Andean rivers is 18 (Biobío River basin, 24.000 km^2 and 380 km length); while, the Andalién River basin of 775 km^2 and 60 km in length, hosted 16 native species according to historical records. Past geological connections may explain this high biodiversity, as coastal rivers could have acted as a refuge for freshwater fish during the Last Glacial Maximum (Smith-Ramírez, 2004). Therefore,

TABLE 2 Comparison of fish assemblage composition in the potamon areas of the Andalién River and Nonguén stream between the 1919 campaigns by Oliver (1949) and the ones in 2017 and 2018 (this work). (+: Presence).

Species registered	Andalién River		Nonguén stream	
	1919	2017–2018	1919	2017–2018
Native species				
Geotria australis	+			
Mordacia lapicida	+		+	
Cheirodon galusdae	+	+	+	+
Nematogenys inermis	+		+	
Bullockia maldonadoi			+	
Trichomycterus chiltoni			+	
Galaxias maculatus	+	+	+	
Brachygalaxias bullocki	+		+	
Basilichthys microlepidotus	+	+	+	+
Odontesthes mauleanum	+		+	
Percichthys trucha	+	+	+	
Percilia irwini	+		+	
Introduced Species				
Salmo trutta		+		
Cyprinus carpio	+	+		
Gambusia holbrooki		+		+
Total Native/Introduced	10/1	4/3	11/0	2/1

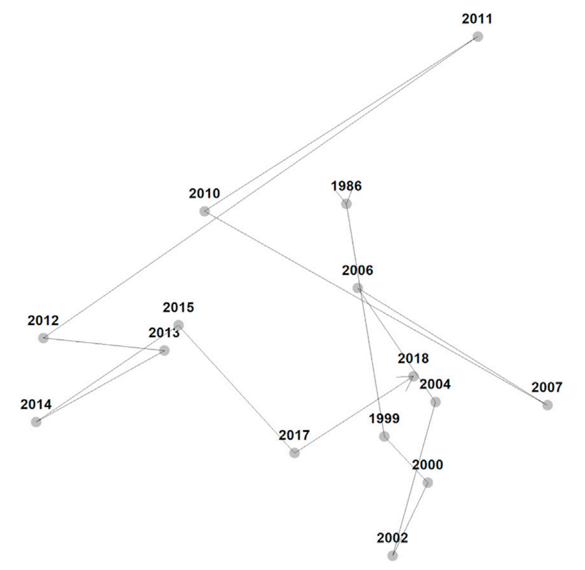

FIGURE 4
nMDS ranking based on the Bray-Curtis dissimilarity matrix on average annual (standardized and transformed) abundances in the Andalién River basin. The trajectory of the fish assemblage structure is shown for 1986–2018. Stress value 0.13.

coastal river basins have a high conservation value but, at the same time, concentrate intensive anthropogenic alterations (Habit and Victoriano, 2005; Habit et al., 2020).

Our results confirm the drastic loss of richness and abundance of native fish species and lampreys in the lower or potamal zone of the Andalién River basin, due to direct alterations in the river ecosystem. Urbanization substantially alters the physical nature of watersheds and waterways through various mechanisms (Marchetti et al., 2006). We attribute the differences in richness and abundance observed in fish assemblages to changes in river morphology that led to the removal of specific habitats and changes in flow, water quality, and sediment regime (Carpenter et al., 2011; Craig and Bonner, 2021). Channelization has numerous impacts on river systems, such as homogenization of river flow velocity, loss of sinuosity, reduction of rapids and substrate types (Huang et al., 2014; Arriagada et al., 2019). In addition to these impacts, the increased catchment imperviousness (Walsh et al., 2005; Engman and Ramírez, 2012) and the extraction of sand and gravel for the execution of the DFWAR project, altered the sediment regimen, resulting in the loss of aquatic habitats (Arriagada et al., 2019). Furthermore, these urban streams often lack riparian vegetation, leading to decreased availability of fish refuge and spawning sites, and loss of habitat for other terrestrial organisms, which are allochthonous food for stream fish (Oscoz et al., 2005; Habit and Victoriano, 2005). The lack of riparian vegetation also affects water quality, increases water temperature, and increases solar radiation (Oscoz et al., 2005). This reduction in environmental complexity or heterogeneity created new homogeneous conditions, often ideal for many exotic fish species (Marchetti et al., 2006), such as *G. holbrooki*, but detrimental to the native fish and lamprey fauna of the Andalién River basin.

In this study, we expected that the direct alterations in the riverbed of the lower potamal zone resulted in a higher impact on the fish and lamprey assemblages. However, the BACI analysis demonstrated species richness reduction at both impacted and control sites. Furthermore, the species richness in the control sites (middle or transitional zones of the river) was higher than in the impacted sites (lower zones) at the beginning of the monitoring. Indeed, this was unexpected since the lower zones of Chilean rivers exhibit the highest species richness of native fish (Habit and Victoriano, 2005; Habit et al., 2006). These results suggest that the river began losing species before 1986, the year used as the starting point for the BACI analysis. Unfortunately, no records exist between 1919 and 1986. However, urban settlement started in the area long before the 1600s (Pauchard et al., 2006; Espinosa et al., 2018). Besides, in the 1900s, Concepción city became an important industrial hub, given its proximity to the Talcahuano port; later, in 1950, the metropolitan areas were strengthened along with forestry development (Pauchard et al., 2006), making species loss

TABLE 3 Similarity percentage analysis (SIMPER) between time periods without direct alteration by dredging (1986–2004) and with alteration (2006–2018) in the lower area of the Andalién River.

Species	Average abundance without alteration (average similarity: 21.47%)	Average abundance with alteration (average similarity: 24.47%)	Average dissimilarity and contribution percentage in parenthesis (average dissimilarity: 80.01%)
C. galusdae	3.42	5.17	14.98 (18.72)
G. maculatus	2.12	2.98	11.34 (14.17)
G. holbrooki	0.56	3.36	11.23 (14.04)
M. lapicida	1.99	0.00	6.56 (8.20)
G. australis	1.95	0.00	6.06 (7.57)
P. irwini	1.85	0.00	5.53 (6.91)
A. facetus	1.24	0.00	4.01 (5.01)

TABLE 4 Similarity percentage analysis (SIMPER) between time periods without direct channelization alteration (1986–2004) and with alteration (2012–2015) in the lower area of the Nonguén stream.

Species	Average abundance without alteration (average similarity: 27.36%)	Average abundance with alteration (average similarity: 12.38%)	Average dissimilarity and contribution percentage in parenthesis (average dissimilarity: 84.38%)
O. mykiss	1.57	0.45	11.55 (13.69)
C. galusdae	1.37	0.78	10.80 (12.79)
T. areolatus	1.60	0.59	10.72 (12.71)
S. trutta	1.45	0.18	9.63 (11.41)
B. maldonadoi	1.05	0.67	8.53 (10.11)
P. irwini	1.24	0.94	8.29 (9.82)

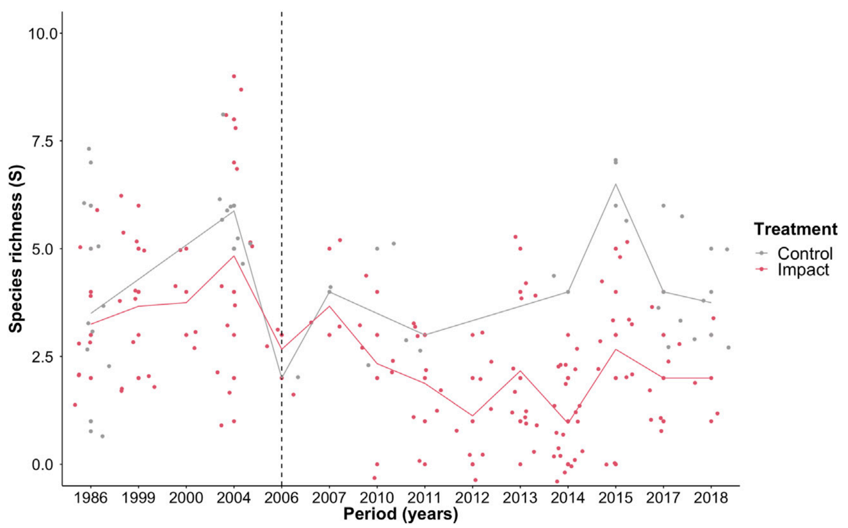

FIGURE 5
Richness of native species at impacted and control sites from Andalién river before and after started fluvial works of DFWAR project from 2006 (dashed line). Gray circles (control sites) and red circles (impact sites) show species richness in each site. Solid lines are moving average for each year for control and impact sites.

TABLE 5 Adjusted mean of species richness and 95% confidence interval for treatment and period.

Treatment	Period	Mean	Lower limit	Upper limit
Control	Before	5.26	3.89	7.11
Impact	Before	3.53	2.68	4.65
Control	After	3.08	2.39	3.96
Impact	After	2.07	1.69	2.53

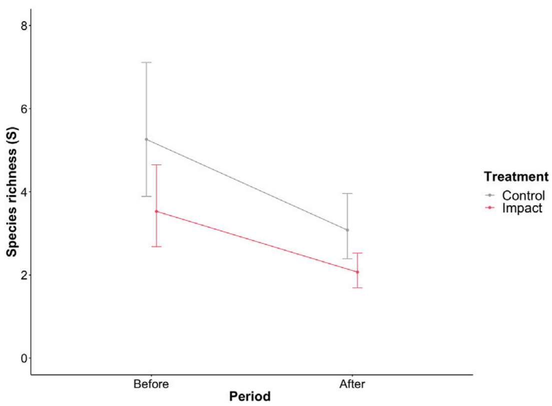

FIGURE 6
Least square means values of species richness before and after DFWAR project. Error bars show the ± CI from the glmer function.

likely before 1986. Furthermore, the reduction in species richness evidenced in the control zone, may be the result of the massive land use change in the Coastal Mountain range, from native forest to agriculture, during the 19th Century. The Coastal Mountain range was called at that time as "El Granero de Chile" ("Chilean wheat bowl"; Escalona and Barton, 2021) since it provided food to most of the country. This situation had to change when soil erosion made it impossible to continue harvesting grains and vegetables. Then, intensive forestry based on monoculture with exotic species started with State subsidies, which has produced extensive land use change throughout the south-central zone of the country (1973 to the present; Torres et al., 2015; Aguayo et al., 2009).

The dramatic collapse in biodiversity showed by our analyses strengthens the idea of loss of resilience of the river ecosystem at a basin scale, and not only in the lower areas most directly intervened. Van Looy et al. (2019) proposed three resilience mechanisms for river ecosystems: resources, recruitment, and refuge. Resource mechanism is related to river productivity. As such, rivers have natural productivity pulses to which communities respond by trophic interactions and abundance adjustments (Connell and Ghedini, 2015). In the Andalién River basin, productivity may have increased due to the continuous nutrient inputs from agriculture and forestry and the increased frequency of non-natural forest fires resulting from monoculture with highly inflammable exotic species like *Pinus* and *Eucalyptus* (Arriagada et al., 2019; de Mello et al., 2022). Recruitment mechanism includes both habitat connectivity and species dispersal ability. Changes in the habitat connectivity of river networks can affect the capacity of species to recruit or recolonize different habitats (Van Looy et al., 2019). The most critical connectivity changes in the Andalién River basin are associated with the DFWAR project in the lower potamal areas. The substantial modifications in the fish assemblage structure immediately at the beginning of the project, as well as the considerable changes in species richness and abundance pre- and post-alterations, suggest that the connectivity alteration was a major stressor for the fish and lamprey fauna. As in other rivers, migratory species were the first to respond, resulting in the extirpation of the two migratory species from the basin (*G. australis* and *M. lapicida,* e.g. Díaz et al., 2021). Finally, the refuge mechanism refers to habitat heterogeneity, which together promotes species survivorship and functional redundancy (Van Looy et al., 2019). Functional redundancy allows compensatory interactions among species in response to environmental fluctuations (Angeler and Allen, 2016; Nash et al., 2016). Direct alterations in the Andalién River and its tributaries, as well as the extensive land use changes in the basin, have reduced habitat heterogeneity. These anthropogenic alterations have deteriorated the environmental conditions in the river ecosystem (Novoa et al., 2020), which may have impacted the functional redundancy of the fish and lamprey fauna, thus contributing to the loss of vulnerable species. In summary, the three resilience mechanisms may be significantly altered in the river basin, preventing the recovery of fish and lampreys' assemblages after new disturbances.

Here we have discussed how changes in fish and lampreys' assemblage structure and their physical habitat, driven by more than a century of anthropogenic alterations, reflect the loss of resilience of the River ecosystem in the Andalién River basin. However, future research should not only consider a taxonomic approach, such as richness or abundance, but also phylogenetic and/or functional trait-based indices, as suggested by Van Looy et al. (2019), given that a taxonomic approach alone does not always capture the aspects of biodiversity most relevant to ecosystem resilience (Mori et al., 2013). Furthermore, functional traits have been shown to react more quickly to anthropogenic alterations, detecting impacts before species loss or extinction occurs (Mouillot et al., 2013). An integrated resilience-based approach is needed to gain a deeper understanding of how ecosystems respond to anthropogenic alterations, which is particularly relevant in ecosystems with multiple stressors, such as the Andalién River basin. This approach will allow taking the appropriate management and restoration measures to achieve ecosystem recovery.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Comité de Ética, Bioética y Bioseguridad de la Vicerrectoría de Investigación y Desarrollo de la Universidad de Concepción.

Author contributions

AV, EH, OR, VHR, and DM contributed to conception and design of the study. EH, AV, and DM processed the experimental data and performed the statistical analysis. AV, EH, PV, and DM verified the analytical methods, drafted the manuscript and designed the figures. DM, EH, OR, AV, and PV wrote the first draft of the manuscript. DM, AM, and GD performed the measurements of fishes. AM and GD were involved in planning and supervised the work. DM, AV, EH, OR, and VHR contributed to the interpretation of the results. All authors contributed to manuscript revision, read, and approved the submitted version.

Funding

Financial support for this work was received from FONDECYT (No. 1190647).

Acknowledgments

We are grateful to the editor and the three reviewers who provided valuable comments and suggestions that improved the quality of the manuscript. Also, we wish to thank FONDECYT (No. 1190647) for financing this work.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.943586/full#supplementary-material

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