

Invasive poeciliids dominate fish community in a highly altered river: insights from a diversity study of riverbank fishes in Mexico



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The presence of invasive species can cause significant changes in native communities and ecosystem functions. Mexico is home to 6% of all known freshwater fish species on the planet, with a high rate of endemism. Due to heavy urbanization, the Mexican Central Plateau has become one of the most densely populated areas in the world, and its Tula River is considered one of the most polluted rivers in Mexico. Our objective was to investigate whether native fish species persist in such adverse conditions and to evaluate the seasonal and spatial distribution of both native and non-native species at three sites along the Tula River. We evaluated environmental characteristics and fish community structure. We found two native species, the black fin goodea (*Goodea atripinnis*) and the yellow shiner (*Notropis calientis*). However, their abundance was extremely low across all sites and seasons. In contrast, invasive poeciliids dominated the communities, accounting for 99.4% of the total abundance. Our results indicate a clear relationship between river characteristics and fish community structure, highlighting the significance of river width, river velocity, temperature, dissolved oxygen, and pH. The prevalence of invasive species underscores the urgent need for conservation efforts aimed to protect and restore native fish populations.

Keywords: Anthropogenic alteration, Goodeids, Invasion success, Tula River.

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La presencia de especies invasoras puede causar cambios significativos en las comunidades nativas y en las funciones de los ecosistemas. México alberga el 6% de todas las especies de peces conocidas en el planeta, con una alta tasa de endemismo. Debido a la fuerte urbanización, el Altiplano mexicano se ha convertido en una de las áreas más densamente pobladas del mundo, y su río Tula es considerado uno de los ríos más contaminados de México. Nuestro objetivo fue investigar si las especies de peces nativos persisten en estas condiciones adversas y evaluar la distribución estacional y espacial de las especies, tanto nativas como no nativas, en tres sitios a lo largo del río Tula. Evaluamos características ambientales y la estructura de la comunidad de peces. Encontramos dos especies nativas, el Tiro (*Goodea atripinnis*) y la carpita amarilla (*Notropis calientis*). Sin embargo, sus abundancias se encontraron extremadamente bajas en todos los sitios y estaciones. En contraste, los poecílidos invasores dominaron las comunidades en todos los sitios y estaciones, representando el 99,4% de la abundancia total. Nuestros resultados indican una clara relación entre las características del río y la estructura de la comunidad de peces, resaltando la importancia del ancho del río, la velocidad del río, la temperatura, el oxígeno disuelto y el pH. La prevalencia de especies invasoras resalta la necesidad urgente de esfuerzos de conservación dirigidos a proteger y restaurar las poblaciones de peces nativos.

Palabras clave: Alteración antropogénica, Éxito de invasión, Goodeidos, Río Tula.

INTRODUCTION

Freshwater ecosystems are under extreme social, political, and economic pressure worldwide, since almost all human activities are closely connected to water (Reid *et al.*, 2019). The environmental and ecological stress in rivers is primarily due to the influence of human settlements, with increased poverty contributing to greater dependency on the ecosystem services provided by water and its nutrients (Kondolf *et al.*, 2018; Best, 2019). The use of water resources imposes numerous modifications to the morphology of rivers, such as the construction of dams and irrigation canals. The quality of water in watersheds is affected by land use, with agriculture, industry, urbanization, and deforestation representing the primary sources of point and diffuse pollution. This, in turn, affects aquifer storage and water quality (Aguilar-Ibarra, 2010).

Anthropogenic alteration of rivers including pollution, overexploitation, habitat modification and the introduction of exotic species, induce changes in rivers that significantly impact their resilience (Arnell, Gosling, 2016). Moreover, some of these stressors act synergistically, with habitat fragmentation and pollution posing a threat to the survival of native species and facilitating the arrival and establishment of exotic species that can later become invasive. These invasive species often possess traits that enable them to thrive and dominate in human-disturbed environments. As a result, they can outcompete native species, potentially causing further ecological imbalances (Simberloff *et al.*, 2013).

The presence of invasive species often results in a significant alteration of native communities and ecosystem functions, which in turn results in biodiversity losses and ecological integrity through predation, competition, disease transmission, and habitat degradation (Early *et al.*, 2016). These changes lead to important economic costs, more than US\$26 billion annually (Diagne *et al.*, 2021), and an interruption in productivity and nutrient availability cycles within the habitat, affecting trophic structure and population dynamics (Parker *et al.*, 1999). The introduction and establishment of invasive species can have almost immediate ecological effects and economic consequences that are increased by the interconnection between rivers (Bernery *et al.*, 2022).

The conservation status of freshwater ecosystems in Mexico is critical, as evidenced by the fact that approximately 70% of water bodies are contaminated to some degree by urban and industrial discharges (Conagua, 2018). Furthermore, almost half of the rivers and streams in the country are classified as having a high or very high degree of ecohydrological alteration (Garrido *et al.*, 2010). Water pollution in Mexican rivers is caused by various sources, such as the discharge of urban waste, including pharmaceutical products, mining (which contribute with heavy metals) and agricultural activities that involve the use of harmful pesticides (Balderas *et al.*, 2017).

Freshwater fish species have been relatively neglected in terms of conservation efforts (Beltrán-López *et al.*, 2023). This lack of attention has resulted in these species being among the most threatened in the context of global change. With around 506 species distributed in 47 families, Mexico represents 6% of the total known species on the planet, with a high rate of endemism (163 species, 32%) (Dudgeon *et al.*, 2006). Despite their importance, Mexico's freshwater fish diversity faces significant threats. For instance, at least 33% of these species are considered at risk of extinction (De la Vega-Salazar, 2006). The Mexican Central Plateau is home to 11 families, of which the Goodeidae family is the highest in endemism with 36 species (Domínguez-Domínguez *et al.*, 2006). Unfortunately, almost all Goodeidae species are in protected conservation status, and some are already extinct in the wild (Suárez-Rodríguez *et al.*, 2023).

The Mexican Central Plateau is highly urbanized, leading to contamination from wastewater, agricultural, and industrial activities associated with major cities such as Mexico City (UN, 2019). Consequently, the Moctezuma River basin is considered the most impacted by human activities in the country (Gutiérrez-Yurrita *et al.*, 2013). Furthermore, the establishment and dispersion of invasive species, loss of habitat, and restricted or specialized tolerance ranges also threaten the permanence of native species in the area (Magurran, 2009; Carrillo, García, 2015; Gesundheit, Macías-García, 2018).

Poeciliids are among the most widespread invasive freshwater fish in the Mexican Central Plateau, they are small viviparous fish that share some ecological requirements with some native species like Goodeids. One of the most researched poeciliids is the guppy *Poecilia reticulata* Peters, 1859, which was introduced to the region in an attempt to control mosquito larvae and as the result of discarding unwanted pets (Azevedo-Santos *et al.*, 2016). This is a species with a natural range of distribution in Trinidad, Guyana, Venezuela, and Suriname (Magurran, 2005), but it is currently present in all continents except Antarctica (Deacon *et al.*, 2011). Although the guppy is a well-known invasive poeciliid in the Mexican Central Plateau, it is not the only invasive poeciliid species in the region. For instance, the twospot livebearer *Pseudoxiphophorus bimaculatus* (Heckel, 1848) and the porthole livebearer *Poeciliopsis gracilis* (Heckel, 1848) are also

found in the Tula River (Camacho–Cervantes *et al.*, 2019). Like guppies, these species have high reproductive rates and phenotypic plasticity, which enables them to establish and grow populations quickly (Gómez–Márquez *et al.*, 2007). Poeciliids mainly inhabit rivers and shallow ponds and possess many physiological, behavioral, and life history traits associated with a broad habitat range (Camacho–Cervantes *et al.*, 2018; Aceves–Fonseca *et al.*, 2022). In contrast, native species tend to have slower reproductive rates and be highly specialized, putting them at a disadvantage when facing a poeciliid invasion (Lyons *et al.*, 2019; Ramírez–García *et al.*, 2020).

The Tula River stands out as one of Mexico's most anthropogenically altered rivers, contending with the inflow of all wastewaters from Mexico City and industrial discharges from Tula City (Ortiz–Gallarza, Ramírez–López, 2003; Casanova *et al.*, 2008). Its water plays a crucial role in irrigating the Mezquital Valley and eventually finds its way to the Zimapán dam (Rubio–Franchini *et al.*, 2016). Previous studies in the region have shown that the Tula River has the lowest species richness and abundance among water bodies in the Moctezuma River basin (Gutiérrez–Yurrita *et al.*, 2013). In our study, we selected three specific sites along the Tula River to investigate whether native fish species persist in such adverse conditions and to evaluate the seasonal and spatial distribution of both native and non-native species at three sites along the Tula River.

MATERIAL AND METHODS

Study area. The Tula River runs from the state of Estado de Mexico to the central-southern region of Hidalgo, plays a crucial role in the Panuco Hydrological Region which flows into the Gulf of Mexico (Rubio–Franchini *et al.*, 2016). Three distinct study sites were chosen along this watercourse (Fig. 1): 1) Dam spillway (20°09'58"N 99°21'29"W) is situated at the spillway of Endho Dam, influenced by both excess overflow and seepage. Endho Dam receives sewage from Mexico City through both the Central Emitter and the East Emitter. Additionally, it receives discharges from the industrial and urban areas of Tula City, as well as from a refinery and a thermoelectric power plant. Locals commonly describe this dam as an “environmental hell” due to the severe pollution; 2) Spring-fed (20°10'50"N 99°20'26"W) is located downstream from Endho, alongside Binola town. This site is situated in a region abundant with natural springs, contributing to enhanced water quality. The area is surrounded by crop fields, utilizing water for various agricultural activities; 3) Drainage confluence (20°14'26"N 99°13'48"W) is situated downstream within the urban perimeter of Mixquiahuala town. This site serves as a recreational area for locals. However, it is positioned after the confluence with the Salado River, where Tula River receives the remaining portion of the drainage from Mexico City, previously conveyed through the Grand Canal.

Sampling methods. Sampling was conducted at different time points to capture the varying environmental conditions prevalent during the dry hot season in April, the rainy season in July, and the dry cold season in November, all within the year 2019. Each site was visited and sampled once during each of these three distinct seasons. To comprehensively characterize the environmental conditions of each site, multiple parameters were measured. These parameters included the width of the river (m), the

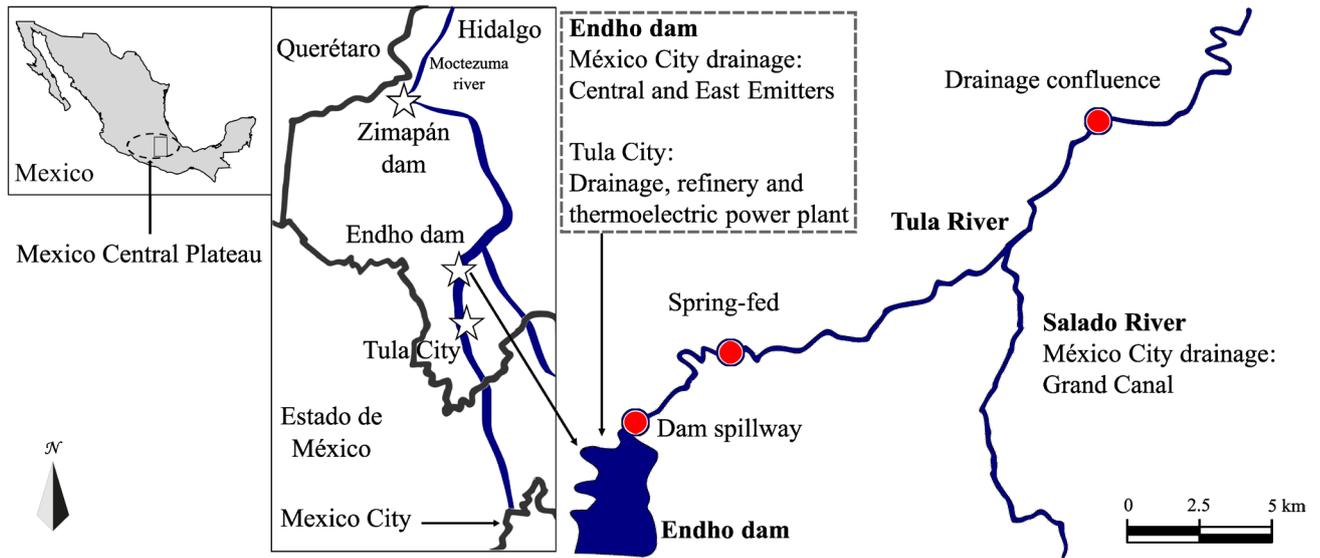


FIGURE 1 | Map of the sampling sites along the Tula River: 1) Dam spillway, 2) Spring-fed, 3) Drainage confluence.

river velocity (m/s), dissolved oxygen concentration (mg/L), temperature ($^{\circ}$ C), and pH. To obtain a representative average of the river's velocity (m/s), we utilized the floating method at various depths (~ 1.2 m) across the river. For measuring dissolved oxygen, a microprocessor-based probe (HI-9146, Hanna Instruments) was employed. Additionally, temperature and pH measurements were obtained using a multiparameter sonde (HI-991300, Hanna Instruments), which allowed for simultaneous data collection. Sondes were placed at 20 cm below water surface. All environmental data were collected at the fish sampling sites and during the same period.

Fish sampling proceeded in a standardized approach following the Standard Methods for Sampling North American Freshwater Fishes (Bonar *et al.*, 2009). Six unbaited Gee's minnow traps (42 cm, 2 mm mesh) with funnel entrance diameter of 3 cm were set for four 15-min periods. Additionally, a single fisher used a hand net (49 x 39 cm, 3 x 4 mm mesh size) to capture individuals within a 30-min period. Sampling was conducted at least three meters away from where the fish traps were placed, and approximately 30 hand net launches were carried out during each sampling event. The section of the river within which the samples were taken covered a length of approximately 30 m in each site.

Sampling sites were selected to cover all possible available habitats along the riverbank. Fish surveys were conducted during daylight hours (between 10:00 and 13:00) from Monday to Friday to avoid interference from recreational visitors. At the end of each sampling period, individuals were collected, identified, and then released on-site to avoid disrupting the community structure. These methods were chosen because in this area the river is relatively small (width ~ 30 m) and shallow (~ 50 cm).

Statistical analyses. The fish data were standardized by sampling time to enable comparison of the percentage of individuals found in each site and season. To ensure the representativeness of the sampling effort, species accumulation curves (SAC) were constructed for each site and season. In order to describe the fish communities, we used species richness, abundance, and calculated Shannon diversity index (H), Simpson

dominance index (D) and beta diversity (Whittaker). To compare the abundance of each species within sites and seasons, rank abundance curves were generated. For the drainage confluence site, a logarithm was applied due to the relatively large number of individuals recorded across all seasons. We performed a Canonical Correspondence Analysis (CCA) to examine the relationships between environmental conditions as explanatory variables and fish abundance as response variables for each site and season. In addition, Pearson correlations were performed between environmental variables and community indexes using data from every site and season. Community analyses were performed using the “vegan” package within the R statistical software (R Development Core Team, 2020).

RESULTS

The fish community along the riverbank consisted of seven species, out of which two were native, namely the blackfin goodea, *Goodea atripinnis* Jordan, 1880, and the yellow shiner, *Notropis calientis* Jordan & Snyder, 1899; and five of them are invasive, the guppy, *Poecilia reticulata*, the twospot livebearer, *Pseudoxiphophorus bimaculatus*, the porthole livebearer, *Poeciliopsis gracilis*, the shortfin molly, *Poecilia mexicana* Steindachner, 1863, and the common carp, *Cyprinus carpio* Linnaeus, 1758. The species accumulation curves for each site and season show that the sampling method was adequate and sufficient (Fig. S1).

The dam spillway site lacked any native species, while in spring-fed and drainage confluence sites, native species were present but in extremely low numbers constituting only 0.64% and 1.09% of the overall abundance, respectively (Tab. 1). Across all sites, the most dominant species was an invasive one: *P. bimaculatus* (dam spillway), *P. mexicana* (spring-fed) and *P. reticulata* (drainage confluence). Overall, invasive species accounted for 99.4% of the total abundance.

TABLE 1 | Species present in the Tula River, the total number of individuals collected at each site and their respective percentages.

| Origin | Species | Dam spillway | | Spring-fed | | Drainage confluence | |
|----------|---|--------------|---------|------------|---------|---------------------|---------|
| Native | <i>Goodea atripinnis</i> (Ga) | 0 | (0%) | 2 | (0.4%) | 104 | (1.1%) |
| | <i>Notropis calientis</i> (Nc) | 0 | (0%) | 1 | (0.2%) | 0 | (0%) |
| | Total | 0 | (0%) | 3 | (0.6%) | 104 | (1.1%) |
| Invasive | <i>Poecilia reticulata</i> (Pr) | 2 | (0.6%) | 100 | (22%) | 9018 | (95.1%) |
| | <i>Poecilia mexicana</i> (Pm) | 23 | (6.9%) | 169 | (37.1%) | 157 | (1.7%) |
| | <i>Pseudoxiphophorus bimaculatus</i> (Pb) | 203 | (61%) | 72 | (15.8%) | 116 | (1.2%) |
| | <i>Poeciliopsis gracilis</i> (Pg) | 105 | (31.5%) | 97 | (21.4%) | 88 | (0.9%) |
| | <i>Cyprinus carpio</i> (Cc) | 0 | (0%) | 14 | (3.1%) | 1 | (0%) |
| | Total | 333 | (100%) | 452 | (99.4%) | 9380 | (98.9%) |

Our data showed that native species are persisting in very low abundances within the studied sites and seasons (Fig. 2; Tab. S2). In dam spillway site, the native species were absent. In spring-fed site, both native species were present, but with *G. atripinnis* observed only during the rainy season and *N. calientis* during the dry hot season. In drainage confluence site, *G. atripinnis* was present during all three seasons, but in relatively low numbers in contrast with invasive species. In dam spillway site, *P. bimaculatus* dominated during both dry hot and rainy seasons, while during the dry cold season, *P. gracilis* dominated. Similarly, in spring-fed site *P. mexicana* dominate during the same dry hot and rainy seasons, while *P. reticulata* dominated during the dry cold season. Interestingly, in drainage confluence site, *P. reticulata* dominated in all three seasons.

Among the different sites, dam spillway had the lowest species richness and abundance, while spring-fed showed higher numbers and even more so in drainage confluence (Tab. 2). However, drainage confluence site exhibited the lowest values of diversity and highest of dominance, with *P. reticulata* being the most abundant species across all seasons. In contrast, spring-fed site showed the evenest distribution of species, with the lowest dominance index recorded being 0.31 during the dry hot season. The analysis of beta diversity revealed that, overall, there is greater spatial than temporal variation in species composition (Tab. S3). The site with the greatest difference was the dam spillway during the dry cold season, as only two species were recorded: *P. gracilis* and *P. reticulata*. High similarity was observed between the dam spillway during the dry hot and dry rainy seasons, as well as among the three seasons of the drainage confluence site. Among sites, there was a notable similarity between spring-fed during the rainy and dry cold seasons and drainage confluence across all three seasons.

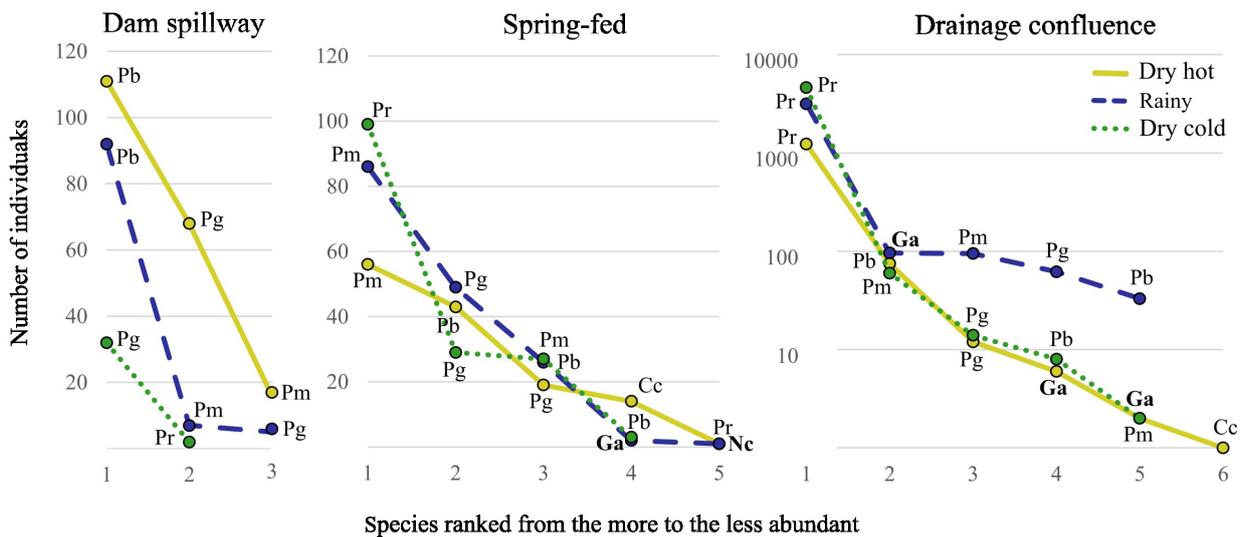


FIGURE 2 | Rank-abundance curves for each site and each sampled season. Pb: *Pseudoxiphophorus bimaculatus*; Pr: *Poecilia reticulata*; Pg: *P. gracilis*; Pm: *P. mexicana*; Ga: *Goodea atripinnis*; Nc: *Notropis calientis*, Cc: *Cyprinus carpio*. Native species are highlighted in bold. Due to the high number of individuals in drainage confluence site Log10 was used for comparative purposes.

TABLE 2 | Environmental characteristics and community indexes for each site and season.

| | Dam spillway | | | Spring-fed | | | Drainage confluence | | |
|----------------------|--------------|-------|----------|------------|-------|----------|---------------------|-------|----------|
| | Dry hot | Rainy | Dry cold | Dry hot | Rainy | Dry cold | Dry hot | Rainy | Dry cold |
| River velocity (m/s) | 0.02 | 0.06 | 0.08 | 0.02 | 0.02 | 0.02 | 0.35 | 0.33 | 1.33 |
| River width (m) | 38 | 28.8 | 29 | 40 | 32.2 | 33 | 35 | 28.8 | 28.7 |
| pH | 7.2 | 7.2 | 7.5 | 7.3 | 7.4 | 7.7 | 7.5 | 7.6 | 7.8 |
| Oxygen (%) | 26.9 | 40.2 | 48 | 29.5 | 36.5 | 49.2 | 27.3 | 36 | 40.6 |
| Temperature (°C) | 20.1 | 19.0 | 18.9 | 21.6 | 20.7 | 19.2 | 21.4 | 20.3 | 19.1 |
| Species richness | 3 | 3 | 2 | 5 | 5 | 4 | 6 | 5 | 5 |
| Individuals | 195 | 104 | 34 | 133 | 164 | 158 | 1329 | 3455 | 4700 |
| Diversity (H) | 0.90 | 0.45 | 0.24 | 1.30 | 1.09 | 0.99 | 0.32 | 0.39 | 0.11 |
| Dominance (D) | 0.45 | 0.79 | 0.89 | 0.31 | 0.39 | 0.45 | 0.86 | 0.84 | 0.96 |

Our results indicate significant positive correlations between river width and temperature ($r = 0.70$, $p = 0.03$) and diversity ($r = 0.72$, $p = 0.02$), as well as significant negative correlations with dissolved oxygen ($r = -0.67$, $p = 0.04$) and dominance ($r = -0.73$, $p = 0.02$). Furthermore, the study revealed that the abundance was positively correlated with both river velocity ($r = 0.89$, $p = 0.001$) and pH levels ($r = 0.67$, $p = 0.04$). Additionally, the temperature was positively associated with species richness ($r = 0.69$, $p = 0.03$) and negatively related to dissolved oxygen ($r = -0.80$, $p = 0.009$) (Tab. 2).

The results of Canonical Correspondence Analysis (CCA) provided valuable insights into the relationship between environmental characteristics and fish community structure across different sites and seasons (Fig. 3). The first and second axes of the CCA explained 98% of the total variance (with 76% attributed to CCA1 and 22% to CCA2; Tab. S4). CCA1 positive scores were strongly associated with pH (0.87) and river velocity (0.66), while showing a negative relation with river width (-0.33). These positive components of CCA1 were consistently associated to the presence of *G. atripinnis* and *P. reticulata* and the drainage confluence site throughout all seasons. Conversely, the negative side of CCA1 was associated with the dam spillway site across all seasons, with a prevalence of *P. bimaculatus* and *P. gracilis*. Additionally, the negative side of CCA1 was also linked to the spring-fed site during the dry hot and rainy seasons and with the presence of *N. calientis*, *C. carpio*, and *P. mexicana*. CCA2 positive scores were mainly influenced by Temperature (0.53) and river width (0.41), while displaying a negative relationship with river velocity (-0.2). This allowed for a clear differentiation between the spring-fed and dam spillway sites.

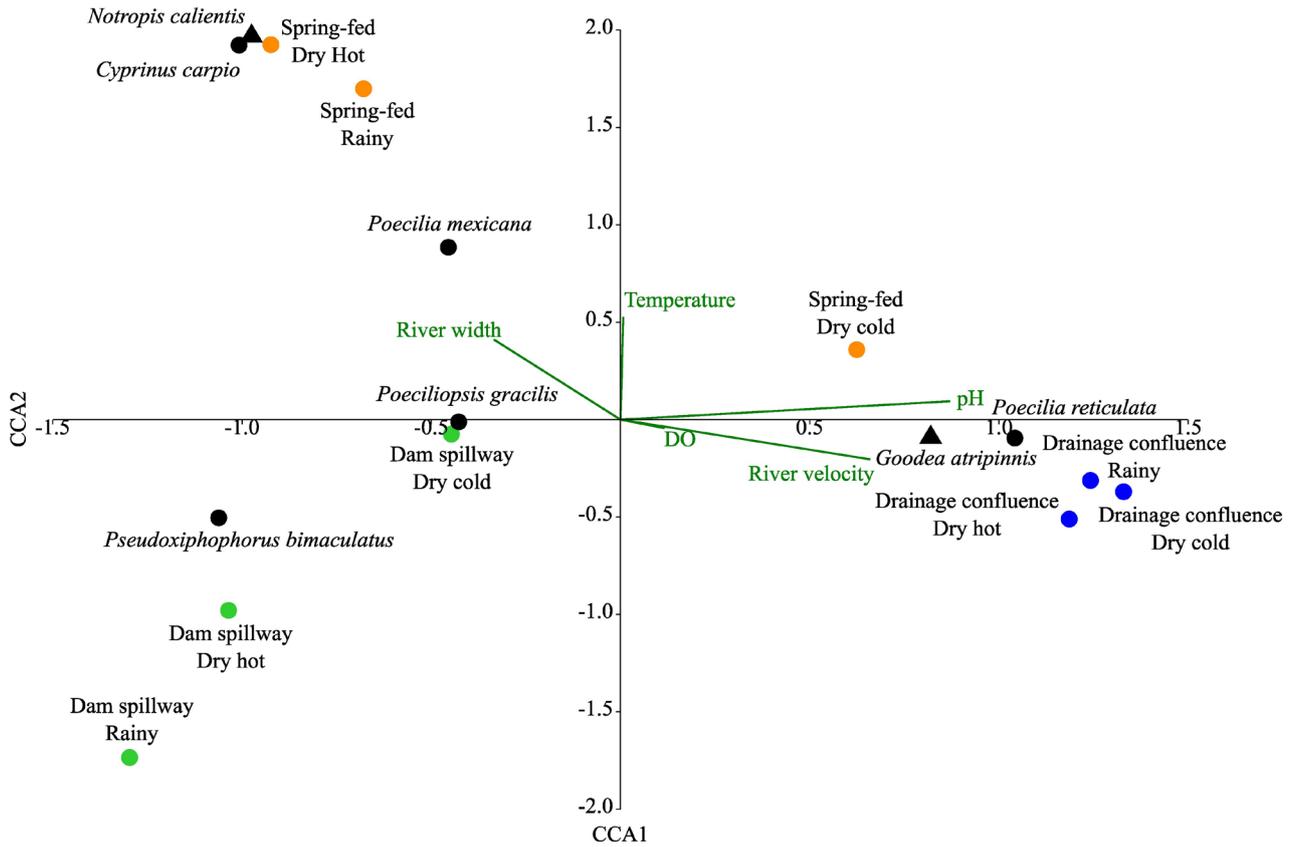


FIGURE 3 | Canonical Correspondence Analysis (CCA) results showing the relative influence of environmental variable on the community structure of fish species within each site and seasons. Native species are represented by black triangles, while invasive species are denoted by black circles

DISCUSSION

We found the Tula River to be extensively invaded, with only two native species persisting: the blackfin goodea (*G. atripinnis*) and the yellow shiner (*N. calientis*), but they only account for a maximum of 1% of total abundances. Historical inventories of native species in the heavily altered Tula River are scarce, hampering a comprehensive understanding of pre-existing biodiversity and its abundance. Our findings confirm a decline in native species likely due to anthropogenic alteration and competition with invasive species.

From the two native species found in our site, *N. calientis* is the rarest. Its conservation status was recently evaluated for the IUCN Red List, where it was classified as Critically Endangered (Domínguez, 2019). Interestingly, *N. calientis* was found only in spring-fed, a site that is influenced by water springs along the riverbed. It was neither found in dam spillway site Endho, where only invasive species were found, nor in drainage confluence site, where the water from Saldo River is incorporated. Considering this, we believe that the subsistence of *N. calientis* is related to some aspects of water quality. Contrastingly, *G. atripinnis* is a widely distributed goodeid species in central Mexico (Miller *et al.*, 2009), it holds a conservation status of Least Concern according to the

most recent evaluation on the IUCN Red List (Koeck, Maiz-Tome, 2019). This species is known for its adaptability to challenging conditions (Ramírez-García *et al.*, 2021) and its reputation as one of the most tolerant species within its family (Silva-Santos *et al.*, 2016) it was encountered in remarkably low abundance only in spring-fed and drainage confluence sites.

The other five species we found in our surveyed sites are widely recognized as invasive in the Central Mexican Plateau (Miller *et al.*, 2009). In all sites, the most dominant species was an invasive poecilid, the specific species varied: *P. bimaculatus* in dam spillway site, *P. mexicana* in spring-fed site, and *P. reticulata* in drainage confluence site. Our data highlights the prevalence of invasive species, constituting 99.4% of the total fish population, posing a significant threat to native fish populations. The presence and abundance of invasive species are of concern because where poeciliids are established, they tend to disperse and colonize new areas naturally (Gomez-Márquez *et al.*, 2016). As poeciliids can achieve a high level of invasiveness because they are viviparous fish with short reproductive cycles and high fecundity (Ramírez-García *et al.*, 2017). These findings are of concern as invasive species represents one of the most severe and less controlled problems around the country (Contreras-MacBeath *et al.*, 2014).

In the Tula River, twospot livebearers (*P. bimaculatus*) dominated the dam spillway site where the species richness was relatively low and only other invasive species were present. This is an invasive species widely spread throughout freshwater ecosystems in central Mexico that can tolerate harsh environmental conditions and could establish widely around the globe (Gomez-Maldonado *et al.*, 2023). Mature females and males of *P. bimaculatus* have been found in degraded sites of rivers where they tend to spread and colonize new areas (Ramírez-García *et al.*, 2017). Furthermore, this species can endure changes in the elements of the trophic web and food availability, as it can feed from terrestrial insects, fish eggs, and fish larvae, therefore it can threaten native fish populations (Carbajal-Becerra *et al.*, 2020). For instance, in other basins from central Mexico *P. bimaculatus* was classified as a threat to *N. calientis* populations through egg predation (Carbajal-Becerra *et al.*, 2020).

Drainage confluence site stands out as a significant site, the prevalence of *P. reticulata* at this site is particularly striking, with a notably higher abundance of this species than observed at other sites, linked to river velocity and higher pH levels. Additionally, drainage confluence site is situated within an urban perimeter and is impacted by anthropogenic influences, especially after the incorporation of the Salado River. Guppies' high dominance is not surprising, given that guppies are known for being successful invaders (Magurran, 2005). They can establish populations in a wide range of conditions (Gibson, Hirst, 1955; Chervinski, 1984; Chung, 2001), manage to survive and settle in changing temperatures (Chung, 2001; Reeve *et al.*, 2014) and salinities (Chervinski, 1984), which may be vastly different from those of their native environment. The species composition observed in our study aligns with the findings of Gutierrez-Yurrita (2013). However, they reported *P. reticulata* a new record for the basin, and it was only present in the middle section of the Moctezuma River, and not in the Tula River. In contrast, we found *P. reticulata* in all three sites and was dominant in drainage confluence, suggesting that the species has expanded its territory in recent years. *P. reticulata* is a very social species that derives benefits from associations with natives (Camacho-Cervantes *et al.*, 2015) and other poeciliid invaders (Santiago-Arellano *et al.*, 2021), such as transmission

of information and foraging efficiency or boldness increase. If this were a trend also for the other species found, we hypothesize that twospot and porthole livebearers could also be gaining benefits from associating with natives (Camacho-Cervantes *et al.*, 2023) as well as following an invasive meltdown trend, thus increasing the likelihood of exotic species becoming successful when establishing in an already invaded ecosystem (Simberloff, 2006; Green *et al.*, 2011). However, the geometry of propagule pressure can also play a role (Cassey *et al.*, 2018). Unfortunately, there is no available record of the succession of species invasion in the river.

Spring-fed site presented the highest richness and diversity, indicating a relatively even distribution of abundance. In this site, *P. mexicana* was the most abundant species. Notably, this site was the only site where all seven species were recorded. This may be due to the presence of water springs in the nearby area, which may improve water quality, potentially impacting community structure. Additionally, it is the only site where both native species were present, this may suggest that water springs could positively influence the community structure. For example, in another freshwater site with water springs in the center of Mexico, La Mintzita, the fish community includes 13 fish species, of which four are exotic (Marín-Togo, Blanco-García, 2009).

The differences observed in the community structure of fish suggest that environmental factors are affecting fish populations in the Tula River. Ecosystem alteration can facilitate the establishment of invasive species and these species, in turn, can impact water quality, generating a synergistic effect on native species populations (Reeve *et al.*, 2014). The observation of different invasive poeciliid species dominating at various sites is intriguing and suggests that several factors may contribute to their distribution patterns. These species likely exhibit distinct habitat preferences and environmental tolerances. For instance, *P. reticulata* appears to be associated with higher pH and river velocity, while *P. bimaculatus* and *P. gracilis* were related to lower pH and colder temperatures, and *P. mexicana* was associated with higher temperatures and lower river velocity. Differences in species dominance further underscore the potential impact of competitive interactions among poeciliids. To understand the mechanisms behind these trends, further investigation is necessary. This may involve conducting additional field surveys to study the ecological conditions and resource availability at each site, as well as performing controlled laboratory experiments to assess the competitive interactions between different poeciliid species.

Our results indicate a clear relationship between river characteristics and fish community structure, highlighting the significance of river width, river velocity, temperature, dissolved oxygen, and pH. Specifically, we found that wider rivers tend to host higher species diversity this may be due to the availability of diverse habitats and microhabitats that can support a variety of species with different ecological niches (Ramírez *et al.*, 2022). River velocity and pH demonstrated significant correlations with the abundance of individuals, particularly seem to be favoring *P. reticulata*, which dominated the drainage confluence site consistently across all seasons. Additionally, our analysis indicates a significant positive relationship between temperature and species richness. However, it is crucial to acknowledge the influence of other factors like habitat complexity and nutrient availability, which are commonly linked to warmer environments (Caissie, 2006). Furthermore, the significant negative relationship between temperature and dissolved oxygen is consistent with the widely recognized

phenomenon that warmer water holds less dissolved oxygen, potentially leading to stress for aquatic organisms (Córdova-Tapia *et al.*, 2018). This finding holds particular significance in the context of climate change and the anthropogenic impacts on aquatic ecosystems (Daufresne, Boet, 2007).

Achieving a comprehensive understanding of water quality necessitates a more specific and in-depth study, involving the monitoring of a broader array of water quality parameters at increased frequencies and over extended durations. For instance, within this particular system, we observed greater spatial than temporal variation in species composition, which can be attributed to anthropogenic alterations. Conducting a study of this nature can be highly complex due to the diverse range of biological, chemical, and physical factors that interact in the river. As such, it is crucial to consider the presence of heavy metals, residues from petroleum refining industry, pharmaceutical products, pesticides, and other emerging contaminants that may affect the community structure (Ortiz-Gallarza, Ramirez-Lopez, 2003; Rubio-Franchini *et al.*, 2016; Díaz, Peña-Alvarez, 2017). Nevertheless, the presence of native species has been documented, making it worthwhile to comprehend the factors driving the success of invasive species and develop sustainable approaches to control their spread and reduce their negative effects.

Invasive species have become crucial in the study of aquatic systems as they frequently outcompete native species, particularly in polluted habitats (Bourret *et al.*, 2008; Gomes-Silva *et al.*, 2020). In this case, the native species in Tula River face a double pressure of anthropogenic alteration and invasion, which can act synergistically (Cazzolla-Gatti, 2016; Camacho-Cervantes, Wong, 2023). The Tula River, despite being highly polluted and invaded, presents a significant opportunity for restoration due to its surroundings and the importance of reusing wastewater from major cities, as has been successfully done in other countries (Bain *et al.*, 2014).

The rapid loss of species and habitats in the region has raised concerns regarding the need to protect and conserve ecologically important areas and species (Gutiérrez-Yurrita *et al.*, 2013). To address these concerns, a basin ecosystem management scheme can be implemented that coordinates the management of public and private economic resources. The National Strategy on Invasive Species in Mexico is a comprehensive plan established by the Mexican government to address the issue of invasive species management. Its main objective is to prevent the introduction and spread of exotic species that may pose a threat to biodiversity and native ecosystems. To achieve this, the strategy focuses on various actions, such as early identification and risk assessment of potential invasive species, implementation of control and eradication measures when necessary, and strengthening cooperation among government entities, academic institutions, non-governmental organizations, and civil society (Conabio, 2010). The dominance of invasive species underscores the need for urgent conservation efforts to protect and restore the native fish populations and prevent the arrival of new exotics (Suárez-Rodríguez *et al.*, 2023). We emphasize the importance of implementing measures to control the spread and impact of invasive species, including monitoring and regulation of species introduction and improved management strategies to promote the conservation of native species. Unless immediate and effective action is taken, the dominance of invasive species will continue to threaten native species in the Mexican Central Plateau.

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AUTHORS' CONTRIBUTION

Fernando Córdova-Tapia: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review and editing.

Vianey Palomera-Hernández: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review and editing.

Morelia Camacho-Cervantes: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing-original draft, Writing-review and editing.

Neotropical Ichthyology

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ETHICAL STATEMENT

All fish were treated according to the Official Mexican Standards for the humane treatment of animals during collection (NOM-051-ZOO-1995 and NOM-062-ZOO-1999).

COMPETING INTERESTS

The author declares no competing interests.

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