

Review Article

Long-term evaluation of the impact of urbanization on native and non-native fish assemblages

Shubha N. Pandit^{1,2,3}, Mark S. Poesch², Jurek Kolasa⁴, Laxmi Koirala Pandit^{1,5,6}, Jonathan L. W. Ruppert^{7,8}, Eva C. Enders^{1,9}

¹ Fisheries and Oceans Canada (DFO), Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

² University of Alberta, Department of Renewable Resources, 751 General Services Building, Edmonton, AB T6G 2H1, Canada

³ Current address: Yakama Nation Fisheries, P.O. Box 151, Toppenish, Washington, 98948, USA

⁴ McMaster University, Department of Biology, Hamilton, ON L8S4K1, Canada

⁵ Department of Geography, Planning and Environment, Concordia University, 1455 Boulevard de Maisonneuve Ouest, Montréal, QC H3G 1M8, Canada

⁶ Current address: John I. Haas, 1600 River Road, Yakima, Washington, 98902, USA

⁷ Ecosystem and Climate Science, Toronto and Region Conservation Authority, 101 Exchange Avenue, Vaughan, ON L4K 5R6, Canada

⁸ Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada

⁹ Current address: Centre Eau Terre Environnement, Institut national de recherche scientifique (INRS), 490, rue de la Couronne, Québec, QC G1K 9A9, Canada

Corresponding author: Shubha N. Pandit (shuba.pandit@gmail.com)



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Abstract

Urbanization often leads to the homogenization of species composition in aquatic ecosystems, as it introduces disturbances that can destroy the habitats of unique endemic or native species while creating alternative habitats for species capable of adapting to these conditions. This study utilized a long-term dataset from 1971 to 2010, focusing on fish species presence within three watersheds of the Greater Toronto Area, Canada. The objective was to evaluate any changes in fish communities over time across three groups of species assemblages: native, non-native species, and a combining of all species. We considered key predictor variables for which data exist: catchment area, distance to a species pool source (Lake Ontario), and percentage of urban cover, to determine their impacts on species richness over time. Three hypotheses were tested: (1) the rate of change in species richness differs among the three groups; (2) urbanization promotes the spread and homogenization of non-native species distribution; and (3) native species assemblages exhibit high nestedness initially, decreasing over time as non-native species established and replaced native species. We used general linear models and the nestedness analysis to characterize matrices of species distributions of native and non-native fish assemblages among the catchments over time. Overall, the results indicate that nestedness temperatures (*NTs*) for native fish were lower compared to non-native fish assemblages. Over the four decades studied, native species richness declined with increasing urban cover, while non-native species richness increased and compensated for native losses. Furthermore, native species assemblages exhibited high nestedness at the beginning of the record period, which decreased over time as non-native species became established and replaced native species. This trend suggests that further changes in fish communities are probable. As native fish communities become patchier (not nested), this process may accelerate, potentially isolating communities and making them more prone to perturbations.

Key words: Beta-diversity, nestedness pattern, fish community, spatio-temporal variation, temporal species composition, vulnerability of assemblages, non-resilience

Introduction

Urbanization's growth, leading to the expansion of large cities, has significantly impacted aquatic ecosystem processes (Aronson et al. 2014). These impacts are particularly evident in channelized stream banks and artificial instream structures replacing and degrading natural habitats. Moreover, urbanization modifies the hydrological regime and increases nutrient, sediment, and pollutant loading, potentially altering fish community composition and wetland function (Lee et al. 2006). For instance, urbanization-induced micro-habitat diversity decline has been linked to the loss of native species in rivers and streams (Dyson and Yocom 2015). Additionally, habitat modifications can result in shifts in species composition within algal, invertebrate, and fish composition (Ricciardi 2001; Tchakonté et al. 2015), potentially facilitating the establishment of non-native species (McKinney and Lockwood 1999; McKinney 2006; Buczkowski and Richmond 2012). While numerous studies have assessed the degree of community deterioration (e.g., Matzen and Berge 2008), the nature and direction of changes remain poorly understood (Rowe et al. 2009). Notably, urbanization can sometimes lead to drastic changes in aquatic ecosystems, creating alternative stable states that hinder recovery (Sudduth et al. 2011).

Urbanization transforms predominantly pervious landscapes, such as natural or agricultural areas, into more impervious and disturbed ones, altering hydrological and ecological processes within watersheds. This transformation introduces changes to environmental conditions and variability at different temporal and spatial scales, potentially driving shifts in species composition and distribution patterns (Ricciardi 2001; Tchakonté et al. 2015). Understanding how urbanization and other critical environmental factors influence the assemblages of native and non-native fish species can aid in identifying mitigation measures for conserving native species. Considering the temporal scale involved in fish dispersal over large areas and local filtering of assembly membership, a multidecadal perspective offers a more comprehensive picture rather than short-term datasets on species distribution.

Habitat specialization of species may also affect their response to habitat alterations (Pandit et al. 2009). Non-native species, in general, exhibit a broader resource range use and tend to tolerate various abiotic conditions and human-induced environmental stressors, making them better competitors, which allows them to better establish themselves in numerous locations compared to native species (Karatayev et al. 2009; Leuven et al. 2011; Verbrugge et al. 2012). Thus, local processes, such as hydrologic and physicochemical regimes, are more likely to govern native species, while regional processes, like dispersal, may govern the occurrence of more tolerant non-native species. Furthermore, several factors can influence fish assemblages in rivers, including the catchment area (Allan 2004), distance to a species pool source (Lyons et al. 2017), and the percentage of impervious area within a catchment (Paul and Meyer 2001; Wang et al. 2020). Changes in land use within the catchment area, mainly through urbanization, can modify the flow of water, sediment, and nutrients into aquatic habitats, thereby impacting aquatic ecosystems, fish communities, and fish populations (Allan 2004). The proximity to species sources also plays a crucial role in influencing the colonization and dispersal of fish species in aquatic ecosystems (Lyons et al. 2017). Closer proximity to species sources can enhance species richness and diversity within fish communities through increased immigration and colonization rates (Lyons et al. 2017). Urban cover, often measured as the percentage of impervious surfaces such as roads,

buildings, and parking lots, serves as an indicator of urbanization intensity within a watershed. This urbanization can have detrimental effects on aquatic ecosystems and fish communities (Paul and Meyer 2001; Wang et al. 2020). Thus, to assess the effects of urbanization on the fish assemblages and based on their relevance to urbanization-induced habitat modifications, including an assessment of the importance of catchment area, distance to a species pool source (Lake Ontario), and the percentage of urban cover (impervious area within a catchment), will be important to build an improved understanding of potential drivers of fish assembly change.

Nestedness is a measure of order in an ecological system, and the nestedness analysis is a widely used method for assessing complex spatial and temporal dynamics of ecological communities, provides comprehensive insights into species richness patterns, and the factors influencing local community structure (Cutler 1994; Wright et al. 1998; Azeria 2004; Greve et al. 2005; Azeria and Kolasa 2008; Ulrich et al. 2009; Granado-Lorencio et al. 2012). The concept of nestedness describes the structured arrangement of biodiversity within a specific landscape or geographical area, offering valuable insights into the nature and underlying causes of biodiversity restructuring. Nestedness patterns in a landscape often arise due to differential colonization abilities of species and selective extinction, where species disappear or colonize from different habitats in roughly the same order. Additionally, nested patterns may emerge from habitat generalists occurring in most habitat patches, while specialist species are limited to a few suitable habitats. In nested communities, the species found in smaller areas is a proper subset of those found in bigger areas (Greve et al. 2005; Ulrich et al. 2009). In contrast, no clear hierarchical pattern in species composition appears to occur between different habitats in non-nested assemblages. Species found in one habitat may not necessarily occur in another, and there may be no consistent pattern of species turnover. Here the inconsistency can indicate a more random or idiosyncratic distribution of species across different habitats (Ulrich et al. 2009 and Pritt et al. 2015).

In this study, we aim to assess the level of nestedness in fish assemblages and examine changes in nestedness over a long-term period (1970–2010) in three watersheds within the Greater Toronto Area (GTA), Ontario, Canada. Further, we sought to identify critical variables (catchment area, distance to species pool, and impervious cover) shaping fish communities in highly urbanized systems within the GTA and determine whether their importance varies over time. We also compared and analyzed nestedness patterns between sets of native and non-native fish species to understand potential variations over time that may indicate differential responses of these two species pools. Altogether, our analysis is guided by three primary hypotheses: first, that the rate of change in species richness would vary among native, non-native, and combined species assemblages over time; second, that urbanization would facilitate the spread and homogenization of non-native species distributions across the study area; third, native species assemblages exhibited high nestedness initially, decreasing over time as non-native species established and replaced native species. By addressing these, we aimed to gain valuable insights into the dynamics of fish assemblages in the GTA and the influence of urbanization on their composition and structure.

Material and methods

Study area and fish sampling

The Greater Toronto Area (GTA) in Ontario, Canada, which includes the City of Toronto, the fourth largest city in North America, represents a convenient system to study the long-term impacts of urbanization on fish community composition. For our analysis, we used a comprehensive dataset covering 40 years and 16

subwatersheds within three watersheds in the GTA (Fig. 1). Notably, the GTA's surface area has approximately doubled from 1985 to 2013, and urban expansion will continue due to population growth (Wang et al. 2014; MoF 2013). Here the study area encompasses three watersheds, including Rouge, Don, and Humber rivers (Table 1, Fig. 1). We further divided these watersheds into sixteen subwatersheds using tertiary watersheds (TRCA 2007; TRCA 2008; TRCA 2009a; TRCA 2009b).

We used the fish data from the Ontario Ministry of Natural Resources and Forestry; and Toronto and Region Conservation Authority, following a standardized Ontario Stream Assessment Protocol (Stanfield 2010) from 1970

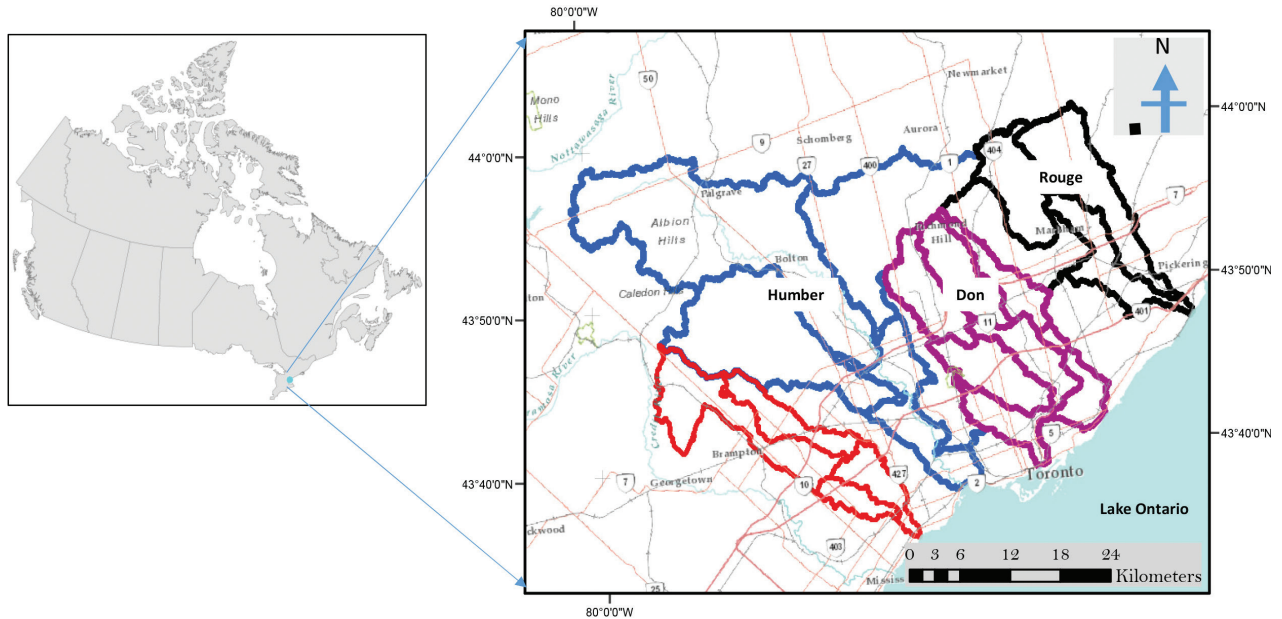


Figure 1. Study area with three watersheds (Humber, Don, and Rouge rivers) within the Greater Toronto Area, Ontario, Canada.

Table 1. Characteristics of the watersheds (Don, Humber, and Rouge rivers) of the Greater Toronto Area (GTA). “catch” represents the catchment IDs and “Distance” represents the distance from the edge of Lake Ontario to the central location of the catchment.

Watershed	catch	Area (km ²)	Distance (km)	Urban percentage (% of impervious area)			
				1970s (1971–1980)	1980s (1981–1990)	1990s (1991–2000)	2000s (2001–2010)
Don	D_s1	60.21	26	36.5	41.0	48.8	58.0
	D_s2	36.48	15	100.0	91.0	89.3	93.8
	D_s3	42.50	25	47.6	58.4	68.9	81
	D_s4	48.28	17	98.1	88.5	88.4	85.7
	D_s5	65.77	18	97.1	88.7	88.6	83.5
	D_s6	62.27	29	20.3	31.9	39.0	68.3
	D_s7	41.24	5.36	100.0	100.0	89.1	86.3
Humber	H_s1	359.43	45.0	1.6	1.9	9.2	30.2
	H_s2	203.98	35.7	7.9	10.6	14.3	28.8
	H_s3	94.11	9.7	76.7	78.6	82.5	83.3
	H_s4	60.56	14.4	77.6	69.9	73.5	84.0
	H_s5	192.01	40.6	3.8	4.8	6.4	22.5
Rouge	R_s1	85.26	29.3	12.9	21.5	33.6	56.8
	R_s2	69.99	25.0	5.2	7.0	3.9	27.2
	R_s3	64.86	7.6	12.9	21.5	30.5	55.9
	R_s4	115.30	10.8	5.3	5.3	1.7	9.0

through 2010. This protocol involves single-pass backpack electrofishing at each site, which samples habitat at a rate of 5 m²·s⁻¹ while systematically moving from downstream to upstream along the banks. The method yields qualitatively repeatable results ($r^2 = 0.90$) relative to multiple pass methods (Reid et al. 2009). To track land use changes over the decades (1960s–2000s), we sourced data from different records: land use data for the 1960s–1980s came from the Canada Land Use Monitoring Program CLUMP (1981), data for the 1990s from the Natural Resources and Values Information System NRVIS (2011), and data for the 2000s from the Southern Ontario Land Resource Information System SOLRIS (2008).

Statistical methods

The sampling site number varied across the 16 subwatersheds and the four time periods in our study (i.e., 1971–1980, 1981–1990, 1991–2000, and 2001–2010). To ensure robustness in our analysis, we randomly selected 25 samples (using stratified sampling) for each catchment and decade, repeating this process 1000 times. This approach allowed us to construct species-sites matrices for each catchment and decade, with columns representing species and rows representing sites. We created separate matrices for each of the three species groups: all species combined, native species only (endemic or indigenous to the region), and non-native species (established in the watershed due to human-driven landscape transformation). The native and non-native fish were separated based on the Ontario Freshwater Fish Life History Database (<https://www.ontariofishes.ca/home.htm>) as well as confirmation through expert opinion specific to the Toronto and Region Conservation Authority.

We first computed species richness (number of species present in each catchment) for each species group and decade. We then used general linear models to assess the relationship between species richness and each predictor variable, aiming to independently determine the explanatory power of significant environmental variables associated with species richness for each decade.

The environmental variables included (1) catchment or river basin area (km²), (2) distance to a significant source or transit of species (measured in meters from the center point of a catchment/river basin to its mouth at Lake Ontario, serving as a proxy for the distance to the source of species), and (3) percent urbanization (representing the percent of impervious area within a catchment). We used the catchment/river basin area as an acceptable proxy for the total water surface within that catchment, as it correlated with the area of water bodies (rivers and streams) within the river basin. To test our first hypothesis, we utilized generalized linear models (GLMs) to assess whether the proportion of non-native species increased over time. In these models, the number of native and non-native species served as response variables, while the decade was the independent variable. Additionally, to test the second hypothesis of whether urbanization facilitated the spread and homogenization of non-native species distributions across the study area, we evaluated changes in community composition over time as the percentage of urbanization increased. We calculated temporal beta-diversity, a dissimilarity measure, between different periods for each of the three groups. The community composition during the earliest decade (1971–1980) served as a benchmark for assessing local community changes in subsequent decades.

For analyzing community nestedness, we used a presence-absence matrix (sites in rows, species in columns, coded 1 for presence and 0 for absence) to calculate nestedness using the BINMATNEST technique (Rodríguez-Gironés and

Santamaría 2006) for each decade. This technique computes nestedness temperatures (NTs) with a Nestedness Temperature Calculator (NTC), measuring the extent of unexpected presence and absence in a maximally packed matrix. The matrix elements are packed by reordering entire rows (sites) and columns (species) to maximize nestedness and minimize unexpectedness. The nestedness temperature (T) ranges from 0° (perfectly nested assemblages) to 100° (complete randomness). Monte Carlo randomizations generated significance tests for nestedness based on the hypothesis that NT is not lower than expected by random chance. BINMATNEST is the most efficient technique for reordering the matrix in this analysis (Rodríguez-Gironés and Santamaría 2006). To test hypothesis three, we evaluated the nestedness temperature between the groups over time to determine whether native species assemblages exhibited high nestedness initially, which decreased as non-native species established and replaced some native species.

Results

In total, we recorded 56 fish species (Fig. 2), with 42 species in the 1970s (1971–1980), 52 in the 1980s (1981–1990), 54 in the 1990s (1991–2000), and 50 in the 2000s (2001–2010). During the 1970s, nine out of 42 species (21%) occurred in more than 75% of the catchments. However, in the subsequent decades (1980s, 1990s, and 2000s), only 13%, 15%, and 16% of the species occurred in more than 75% of the sub-watersheds, respectively (Fig. 2). Five species, including Fathead Minnow (*Pimephales promelas*), Blacknose Dace (*Rhinichthys atratulus*), Creek Chub (*Semotilus atromaculatus*), White Sucker (*Catostomus commersoni*), and Longnose Dace (*Rhinichthys cataractae*), were present in the majority of subwatersheds (>75%) throughout the entire study period.

Rainbow Darter (*Etheostoma caeruleum*), a native species, was common in the 1970s, yet disappeared from many catchments in the 1980s. On the other hand, non-native species in the 1970s were present in less than 30% of the subwatersheds (~five catchments). However, their richness and distribution increased from the 1980s onwards (Fig. 2). We observed that the probability of species occurrence in an area correlated well with its incidence in the preceding decade, although this regularity decreased over time. The analysis of temporal beta-diversity further supported these results, showing that community composition was more similar between adjacent sampling periods than non-adjacent ones (Fig. 3), indicating continuous changes in community composition.

Species richness and the proportion of non-native species increased over time ($r^2 = 0.17$, $P < 0.001$; Fig. 4), suggesting that non-native species are replacing native species. For a one-unit change in species composition in a decade, the odds of observing a non-native species increased by 25%. The relationship between total species richness and predictor variables for each decadal period revealed a consistent trend: subwatersheds with a higher percentage of urbanization had fewer species (Fig. 5C), a pattern observed consistently across all four decades. The catchment area strongly affected species richness, with larger subwatersheds maintaining higher species richness. However, above a specific catchment size, no further increase in species richness took place (Fig. 5A). On the other hand, the impact of distance between subwatersheds and Lake Ontario (the source of species) on the species richness showed no significant trend (Fig. 5B). This suggested that new species did not encounter significant dispersal limitations over decadal time scales, or the fish from lake did not migrate to the stream.

Characteristics of the watersheds (Don, Humber, and Rouge rivers) are in Table 1 and Fig. 6. Although the catchments' size (areas) varied, the impervious area percentage within a catchment showed an increasing trend in most catchments (Table 1, Fig. 6). Overall, fish community structure in the GTA watersheds followed nested patterns rather than random structures across all four decades (1970–2010). However, nestedness temperatures (NTs), a measure of the “heat of disorder,” were lower for native fish [$T=11.01$] than for non-native fish assemblages [$T=24.47$] (Table 2). Native communities were nested across all decades, whereas non-native species exhibited nestedness during only the earlier two decades (Table 2).

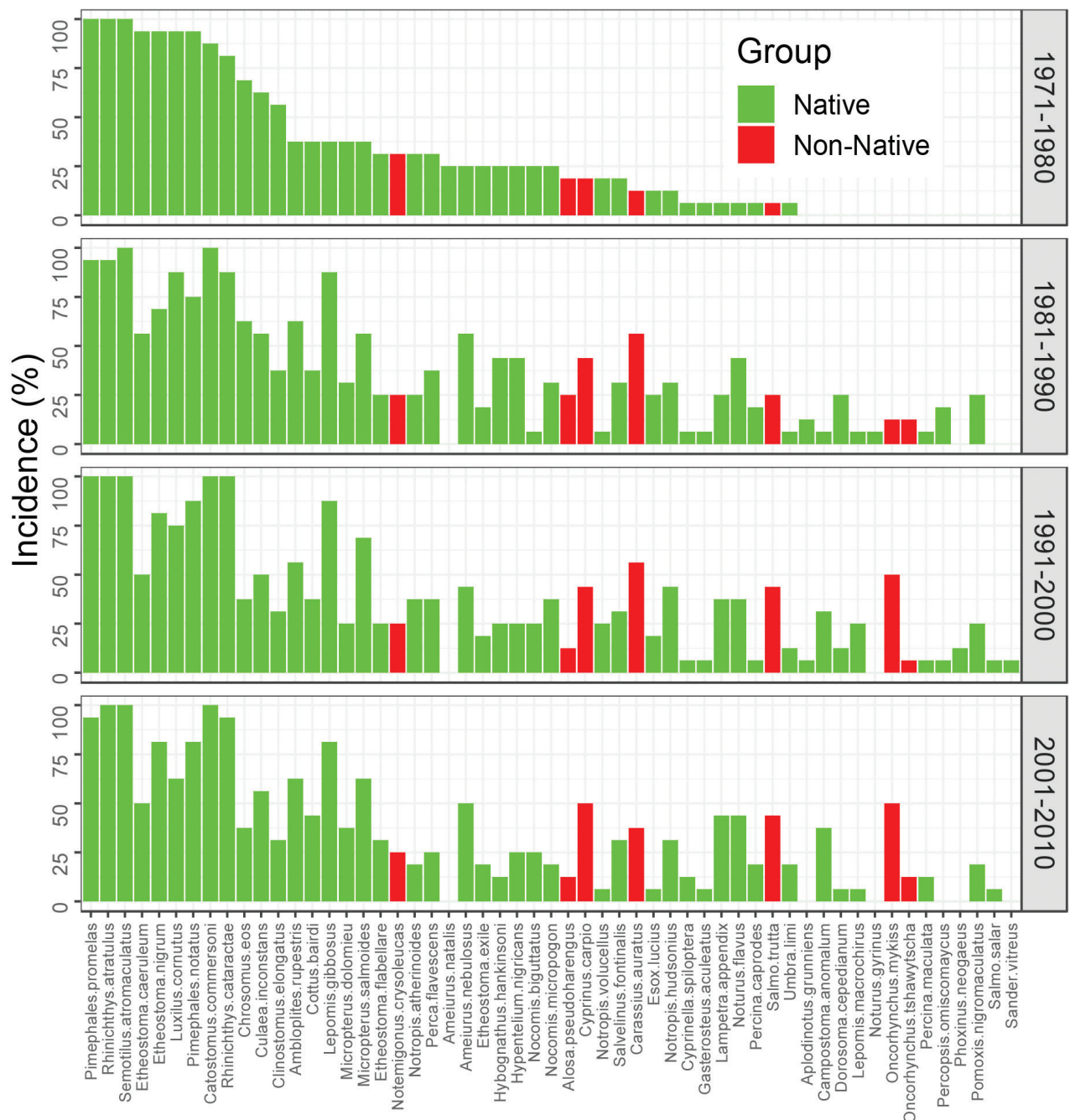


Figure 2. The incidence percentage of different fish species in 16 sub-watersheds in the Greater Toronto Area, Ontario, Canada, during the four decades. The green and red bars represent native and non-native species, respectively.

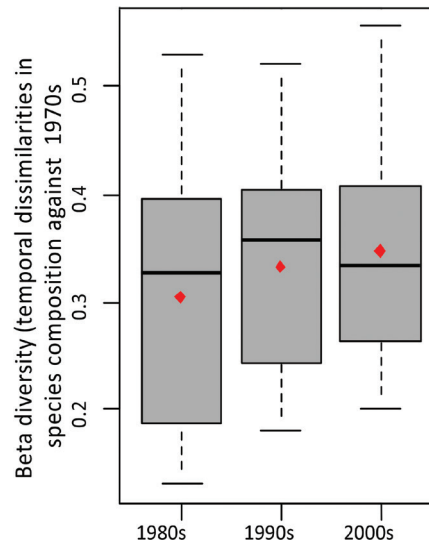


Figure 3. Temporal beta diversity (i.e., temporal dissimilarities in species composition for three decades compared to the benchmark (1971–1980)). Dots in the box plot represent the mean of the dissimilarities with the benchmark.

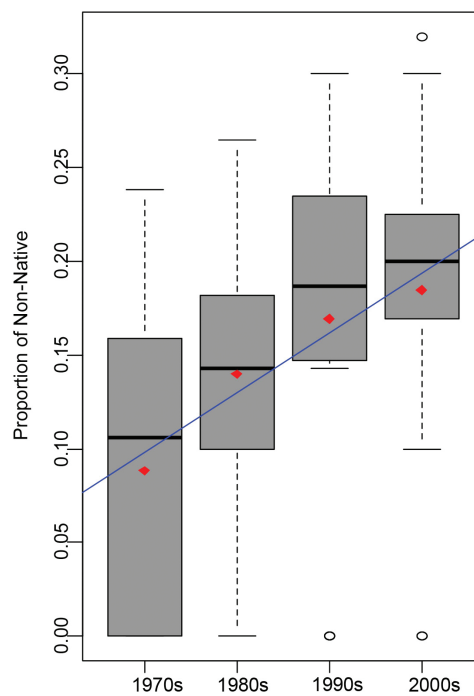


Figure 4. Non-native species proportion within the four decades. The red dot represents the mean value, and the blue line represents the linear trend.

Discussion

Species loss and gain from urbanization

In the four decades (1970–2010), we have observed significant changes in fundamental drivers of freshwater fish assemblages, such as species richness, species composition, hydrological processes, and ecological processes influenced by urbanization. During this period, species richness increased by one-fifth in the study area. However, the ratio of native to non-native species decreased over the same period due to the replacement of native by non-native species. This trend is consistent

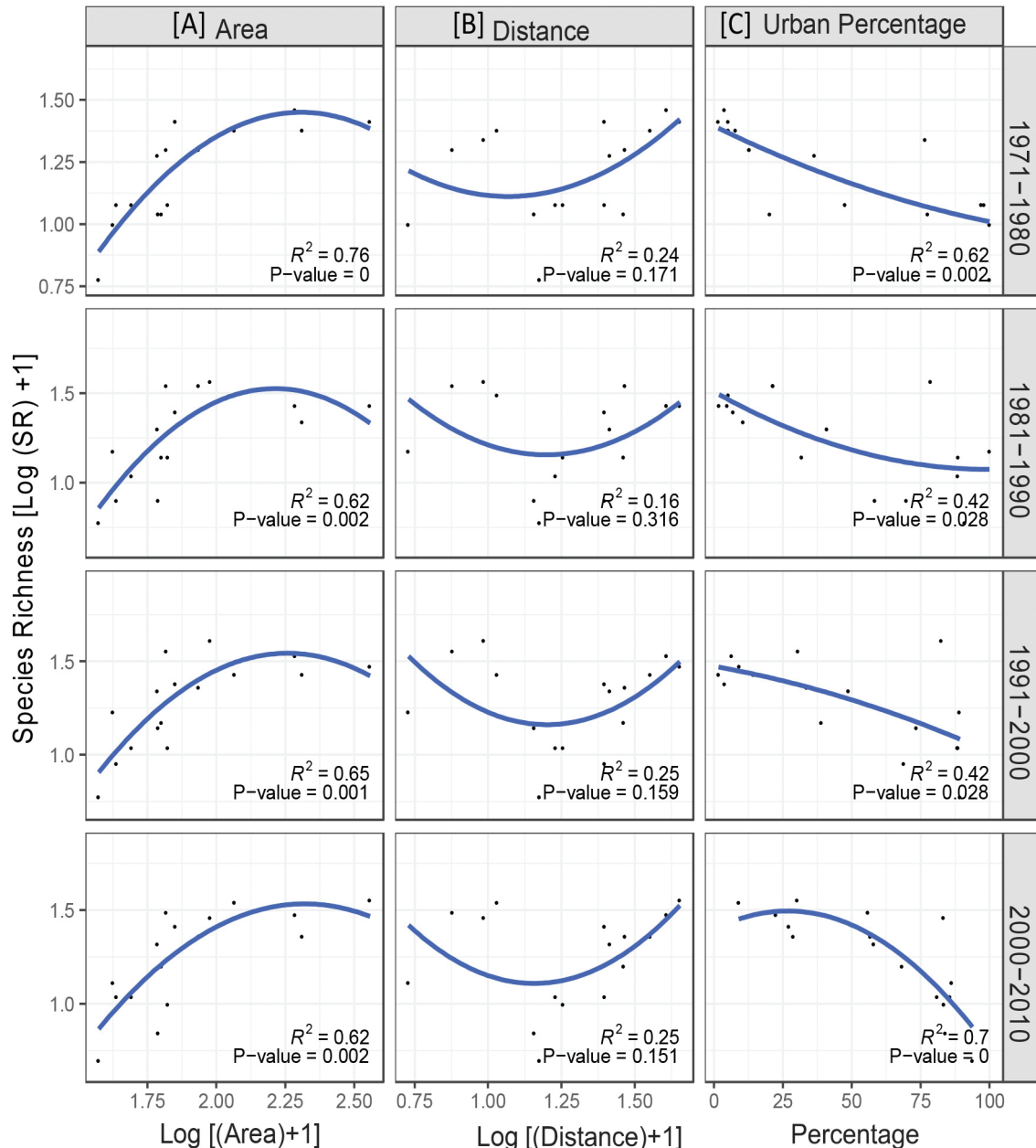


Figure 5. The relationship between (A) species richness and watershed areas, (B) distance from Lake Ontario to the river of each watershed, (C) relative percentage of urban-designated land use in each watershed for each decade.

with the common observation that the arrival and spread of non-native species may pose a significant threat to native biodiversity and aquatic ecosystems (Leprieur et al. 2008; Pandit et al. 2017).

Urbanization is a significant factor contributing to the decline of native species and facilitating the establishment of non-native species. Consequently, areas undergoing extensive urbanization tend to have fewer native species and lower native species abundance (Rickman and Connor 2003). Although some evidence suggests that urbanization can promote biodiversity by increasing species richness, particularly when the number of introductions outpaces species extinctions in specific categories, our study shows that the increase in fish species richness was primarily driven by increasing non-native species. Non-native fish can be predators or prey, however, non-native predators have the potential to negatively affect the abundance and distribution of native species through direct or indirect mechanisms

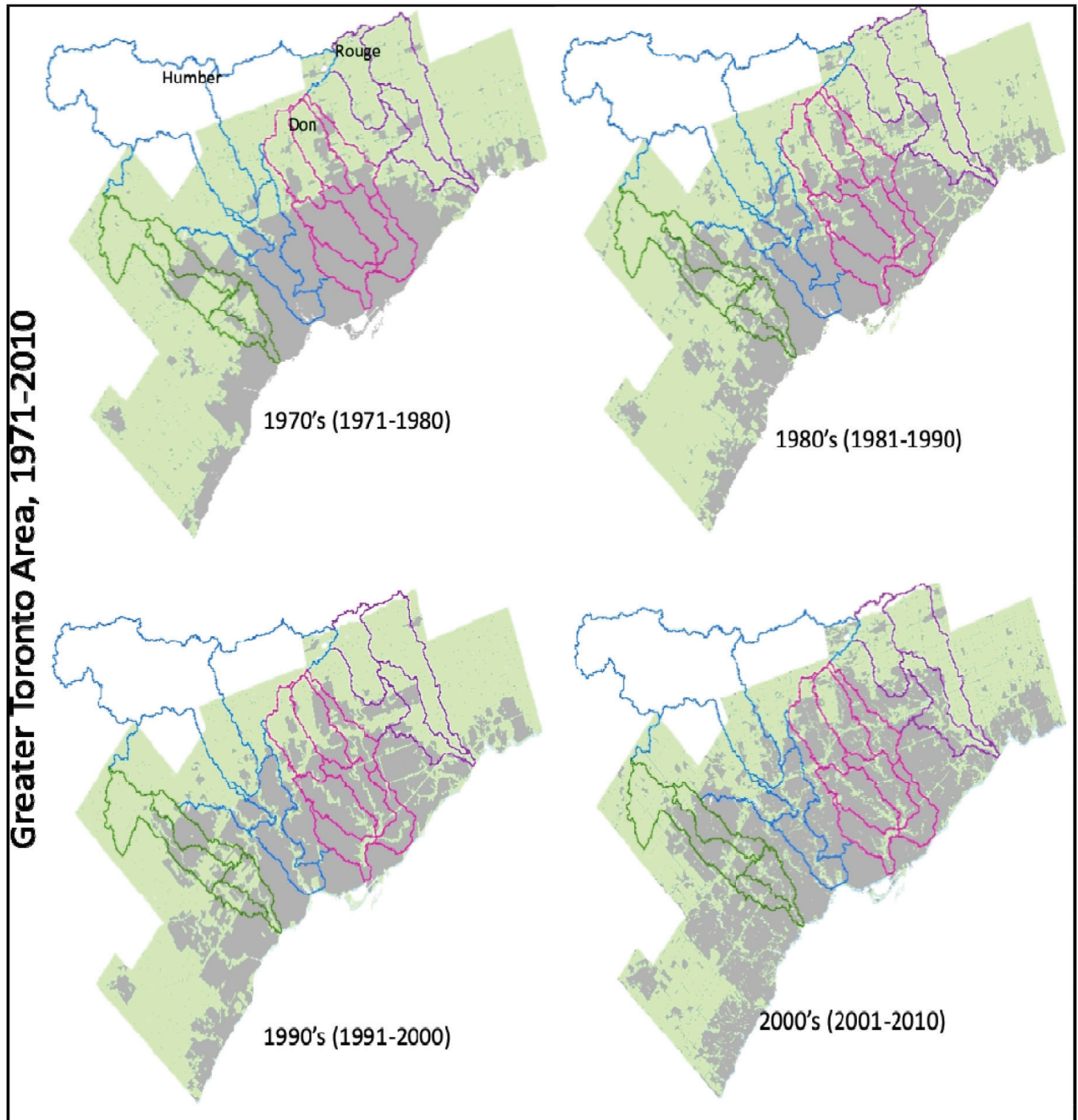


Figure 6. Urbanization of the Greater Toronto Area (GTA), Ontario, Canada covering 16 sub-watersheds of the three watersheds (Humber, Don, and Rouge rivers) from 1970s–2000s. Impervious cover shown in grey, pervious (non-urban) land cover shown in green, and white indicates no classification (insufficient data). Lines delineate the Humber (blue), Don, (pink), and Rouge (violet) watersheds. Land use data modified from CLUMP (1981), SOLRIS (2008), and NRVIS (2011).

such as predation and competition (Hickerson et al. 2019). Furthermore, habitat modifications caused by urbanization may make native assemblages increasingly vulnerable to pressure from non-native species, as non-native species often possess greater adaptability to a broader range of abiotic conditions than native species (Bates et al. 2013).

On a decadal timescale, our analyses revealed species richness changes resulting from species loss (local extinction) and species gain (non-native species) as the common trajectories shaping freshwater fish communities. The resulting structural shifts impact trophic interactions within these communities and significantly

Table 2. Nestedness temperature (*NT*) as an estimate of nestedness BINMATNEST for fish communities for four decadal data sets and all (combined all decadal data set) for each group (combining both the native and non-native; only native and non-natives). Bold values are significant at $p < 0.05$. T_{NM1} , T_{NM2} , and $T_{NM3\pm var}$ is the mean \pm var temperature of the null communities generated under null model 1, 2, and 3, respectively.

Group	Decades	BINMATNEST			
		<i>NT</i> (°)	$T_{NM1\pm var}$	$T_{NM2\pm var}$	$T_{NM3\pm var}$
All	1971–1980	15.90	52.34 ± 27.43	37.14 ± 11.83	40.75 ± 0.02
	1981–1990	11.46	58.09 ± 27.72	34.87 ± 4.90	43.61 ± 9.27
	1991–2000	9.672	58.87 ± 21.78	36.65 ± 6.73	39.72 ± 0.45
	2001–2010	11.92	57.80 ± 12.75	35.97 ± 6.90	41.19 ± 0.50
	Average	12.23			
Native	1971–1980	14.89	53.51 ± 1.76	39.26 ± 3.18	34.92 ± 5.76
	1981–1990	11.29	58.49 ± 36.52	37.79 ± 0.84	39.11 ± 4.41
	1991–2000	8.39	57.22 ± 17.37	41.13 ± 7.96	40.84 ± 20.63
	2001–2010	9.46	56.15 ± 9.02	36.03 ± 6.05	37.24 ± 1.42
	Average	11.01			
Non-native	1971–1980	26.43	21.43 ± 10.76	25.50 ± 183.62	19.15 ± 59.46
	1981–1990	16.37	30.11 ± 26.47	34.33 ± 79.56	36.40 ± 4.82
	1991–2000	25.30	40.19 ± 57.16	27.30 ± 42.92	31.65 ± 15.08
	2001–2010	29.79	35.78 ± 184.52	28.09 ± 180.04	38.82 ± 72.74
	Average	24.47			

affect ecosystem functioning (Estes et al. 2011; Cardinale et al. 2012). Recent research by Maitland and Rahel (2023) further emphasizes that the configuration of food webs along stream gradients is a dynamic interplay between factors that reduce trophic redundancy, such as increased living space and niche partitioning, and factors that enhance trophic redundancy, such as species richness and niche packing. The significant difference in temporal beta-diversity between adjacent and non-adjacent decades indicates that the community composition is shifting over time, providing further support for the inference of compositional uncertainty of communities, which we found in the nestedness analysis (Table 2). Specifically, the nestedness temperature (*NT*) values (nestedness degree) show a declining temporal trend for native species and an opposite trend for non-native species. This trend means that local native assemblages with fewer species are less distinct subsets of larger assemblages than they had in the past. The difference will likely occur when native assemblages undergo more profound compositional restructuring, whereas the opposite temporal trend in non-native species suggests that they gradually establish in most locations suitable for them.

While the fish community of the GTA changed over time, we found that species richness roughly followed species-area relationships and broader expectations (cf., MacArthur and Wilson 1967). Our results suggest that extinction and colonization dynamics play a decisive role in determining species richness in individual subwatersheds, possibly involving risk reduction among the most extinction-prone species provided by large population sizes in large catchments (Boecklen 1997). However, species richness tends to decrease in areas with a higher percentage of impervious land surface within a catchment, indicating that nonpoint source pollution and habitat destruction associated with urban land use can severely affect fish communities. This finding is consistent with other studies, such as the one by Limburg and Schmidt (1990), which found a decrease in spawning habitat and limited recruitment of anadromous fish related to urbanization, where the relationship is clearer when urban land use exceeds 15%.

Nestedness patterns in community composition

In general, the nestedness temperatures (NTs) for native fish were lower than those for non-native fish assemblages. This difference suggests that native fish communities exhibited a higher level of nestedness, where the species found in smaller areas are a proper subset of the species found in larger areas, compared to non-native fish species assemblages. Furthermore, this observation also suggests that non-native species tend to display opportunistic behavior, establishing themselves following their dispersion in locations where their habitat is suitable.

There are other notable differences worth highlighting. Native communities exhibited nestedness consistently across all decades, whereas communities dominated by non-native species did not exhibit nestedness in the 1970s but displayed nested patterns in subsequent periods. This suggests that the initial distribution of non-native species was more unpredictable during the early stages of their spread. Subsequently, non-native species expanded, and their diversity increased during the 1980s, which could have promoted nested patterns through the homogenization of regional assemblages. This homogenization aligns with the observation that effective dispersal and wide distribution often result in high nestedness (Xu et al. 2015).

Furthermore, the catchment area emerged as the primary physical variable promoting regional nestedness, followed by urbanization and isolation from a richer species pool (distance from Lake Ontario to the sub-watershed). Urbanization had a more significant effect on the nestedness pattern of native fish communities compared to non-native fish communities. In contrast, the distance from Lake Ontario had a lesser effect on the nestedness of native species communities than on non-native species. Additionally, it is essential to note that the community compositions of stream and lake environments differ significantly. Even if both habitats are well connected, the species communities cannot be similar due to their distinct habitat conditions.

Nevertheless, the Lake Ontario species pool can enrich associated watersheds by providing a broader selection of candidates tolerating running waters. The effect of urbanization on the nestedness patterns also differed between the two groups (native and non-native species). The nestedness was more pronounced for native species in areas with lower urbanization but less for non-native species. This difference is predictable since non-native species may tolerate a wider range of environmental conditions, use a broader range of resources, and establish populations in more locations than native species, which may have narrower habitat specialization (Traveset et al. 2013).

In summary, the study revealed that species richness increased over time in areas experiencing urbanization, primarily due to the establishment of non-native species. Conversely, the species richness of native species decreased with increasing urbanization. Initially, non-native fish assemblages displayed less nestedness, but over time, they shifted to a nested pattern, indicating the gradual spread of these non-native species throughout the catchments. These dynamics imply a significant likelihood of further changes and a displacement of native species. This information can help identify potential mechanisms that influence local diversity and can aid in conservation efforts.

Authors Contribution

SNP, MP, and ECE formulated the research questions. MP and JLWR assisted in data collection. SNP and LKP analyzed the data, with some support from MP, JK and ECE. SNP drafted the manuscript, and all of us edited it multiple times to improve its quality.

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