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Leaf litter decomposition and macroinvertebrate assemblages along an urban stream gradient in Puerto Rico

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Abstract

Urbanization is a major land use form that has large impacts on ecosystems. Urban development in the watershed impacts stream ecosystems by increasing nutrient and organic matter loads, altering hydrology, and reducing biodiversity. Puerto Rico is an ideal location to assess and monitor the effects of urbanization on streams, because it is increasingly urbanized and streams do not receive inputs of untreated sewage, characteristic of many other tropical urban areas. The objective of this study was to determine how leaf litter decomposition and aquatic macroinvertebrate assemblages varied along a tropical urban gradient. We conducted the study in the Río Piedras watershed, San Juan Metropolitan Area, in six low-order streams that formed an urban gradient ranging from 10% to 70% urban land cover. At each stream, we placed six 5 g leaf bags of *Ficus longifolia* in three different pools and collected one bag on each sampling date. Decomposition rates were fast in forested streams (range 0.021–0.039/day) and decreased with increasing urbanization (range 0.007–0.008/day). Rates were strongly and negatively correlated with percent impervious surface cover ($R = 0.81$, $p = 0.01$). Functional feeding group diversity was higher in forested streams, with the presence of shredders. Decomposition rates were significantly and positively correlated with functional feeding group diversity and abundance ($R = 0.66$, $p = 0.04$). Overall, our results show that urbanization affected the environment and macroinvertebrate diversity resulting in large negative effects on stream ecosystem function.

Abstract in Spanish is available with online material.

KEYWORDS
functional feeding groups, impervious surface, leaf decomposition, macroinvertebrates, Puerto Rico, tropical streams, urban watershed

1 | INTRODUCTION

Urbanization is becoming a dominant land use form worldwide and a major source of stress to stream ecosystems (Paul & Meyer, 2001). In Latin America, 80% of the people live in urban areas, affecting streams via a variety of mechanisms, with increases in impervious surfaces and discharges of polluted water as top stressors (Ramírez, Pringle & Wantzen, 2008; Ríos-Touma & Ramírez, 2019). Major impacts in streams are associated with changes in the physical (e.g., temperature, hydrology, geomorphology), chemical (e.g., nutrient inputs, metals), and biological variables (e.g., introduce species) (Walsh et al., 2005). Those alterations ultimately affect the way ecosystems function (Torres & Ramírez, 2014) (i.e., primary productivity, leaf decomposition, nutrient cycling) and the services they provide (e.g., storm water discharge, recreation, and cultural value). While information on the impacts of urbanization on stream biodiversity has increased in recent years, there is still uncertainty on the mechanisms of how urbanization alters stream ecosystem function particularly in tropical regions (Roy et al., 2016).

Leaf decomposition is a well-studied multistep ecosystem process in forested temperate and tropical streams that allows us to determine and understand the effects of urbanization on stream function (Boyero et al., 2015; Torres & Ramírez, 2014) through a variety of mechanisms. However, we are just beginning to understand how urbanization affects decomposition in tropical environments (e.g., Silva-Junior, Moulton, Boëchat & Gücker, 2014; Torres & Ramírez, 2014). Decomposition rates vary in response to multiple environmental and biological factors, including factors that can be altered by urbanization effects (Boyero et al., 2015; Cook & Hoellein, 2016). Environmental factors, such as warmer water temperatures and higher nutrient levels in urban streams, facilitate microbial colonization and activity on leaves (Fernandes, Seena, Pascoal & Cássio, 2014; Gulis, Ferreira & Graça, 2006). Stream-flow and scouring influence leaf litter breakdown and urban streams tend to have variable and flashy hydrological regimes and leaf breakdown can occur during high flow events (Barnum, Weller & Williams, 2017; Paul, Meyer & Couch, 2006). However, macroinvertebrates are the main consumers of leaf detritus and aid in breakdown rates. As urbanization in a watershed increases, macroinvertebrate groups specialized in consuming leaf detritus disappear affecting the decomposition process (Chadwick et al., 2006). Those factors interact with each other and determine rates at which this process occurs and because functional diversity is regarded as key to understanding ecosystem processes, their response to environmental stress proves to be essential for biomonitoring ecosystem services (Gutiérrez-Fonseca & Ramírez, 2016; Ramírez & Gutiérrez-Fonseca, 2014). Therefore, by assessing leaf decomposition we can evaluate whether stream macroinvertebrate functional diversity and ecological functions are negatively affected by urbanization with an increase in impervious surface cover (Barnum et al., 2017; Cook & Hoellein, 2016; Torres & Ramírez, 2014).

Puerto Rico provides an appropriate scenario to understand the impacts of urbanization on tropical watersheds. The island experienced an accelerated increase in urbanization during the last 60 years, a result from a change in the economy from agricultural to industrial (De Jesús-Crespo & Ramírez, 2011; Grau et al., 2003; Helmer, 2004; López, Aide & Thomlinson, 2001). Currently, 40% of the island is under urbanization or urban sprawl (Martinuzzi, Gould & Ramos González, 2007). Most urbanized watersheds in Puerto Rico have urban centers in low elevations and rural headwaters, creating short-distance disturbance gradients (Torres & Ramírez, 2014). Studies have looked at certain characteristics of the urban impacts on stream ecosystems on the island, such as hydrology (Phillips & Scatena, 2012), water chemistry (Ramírez, Rosas, Lugo & Ramos-González, 2014), microbial communities (Burgos-Caraballo, Cantrell & Ramírez, 2014), macroinvertebrates (De Jesús-Crespo & Ramírez, 2011), and fish assemblages (Engman & Ramírez, 2012). However, we are limited in our understanding of ecosystem processes and their response to urbanization in tropical streams—specifically in Puerto Rico—with only one study assessing leaf decomposition along a land use gradient (Torres & Ramírez, 2014). Contrasting with many tropical regions, most streams in Puerto Rico do not currently receive large discharges of untreated sewage, which is treated in regional plants or contained in household septic tanks, and provide an example of ecosystem responses in the absence of such a large impact (Gutiérrez-Fonseca & Ramírez, 2016; Ramírez & Gutiérrez-Fonseca, 2014).

Here, we studied how urbanization affects an ecosystem process, leaf decomposition, along an urban gradient in Puerto Rico. Our main objective was to assess the effects of increasing urban development on decomposition rates and macroinvertebrate assemblages associated with leaves. We expected to (a) observe a decrease in decomposition rates with increasing urbanization, as well as (b) a decrease in functional feeding group diversity, in particular those that contribute to leaf litter breakdown (i.e., shredders), with an increase in pollution-tolerant species, such as midges, bloodworms, and leeches (De Jesús-Crespo & Ramírez, 2011). Furthermore, we predicted (c) that the decomposition rates will be associated with changes in macroinvertebrate assemblages and FFG diversity (Barnum et al., 2017).

2 | METHODS

2.1 | Study site

We selected six tributaries within the Río Piedras watershed for the study (Figure S1). The watershed drains a large portion of the San Juan Metropolitan Area, Puerto Rico (18°24′23″N, 66°3′50″W), the most urbanized area on the island, with a population density of about 3,190 people/km^2 (U.S. Census Bureau 2010). The watershed has an area 67 km^2, with an elevation ranging from 150 masl in the headwaters to sea level in the bay of San Juan (De Jesús-Crespo & Ramírez, 2011). Average annual precipitation ranges from 1,530 to 1,755 mm, with most of the precipitation becoming runoff due to the high amount of impervious surfaces covering the watershed (Osterkamp, 2001; Potter, Mcdowell, Helton & Daley, 2014). Most streams draining the Río Piedras present some degree of impact due to anthropogenic activities, such as channel straightening and channelization. There is an evident loss of ephemeral and intermittent streams due to construction and urbanization (De Jesús-Crespo & Ramírez, 2011; Lugo, González & Pedraza, 2011). Despite the high degree of urbanization, there are still forest fragments near the streams, especially in the headwaters.

Selected tributaries were low-order streams (2nd–3rd order) that are part of our ongoing urban studies in Puerto Rico. Detailed information on land cover and methods related to watershed metrics are available in Ramírez et al. (2014) and De Jesús-Crespo and Ramírez (2011). The watershed metrics (vegetation cover and impervious surface cover) were obtained using a 4-m resolution land cover classification (American Forests, 2002). Tributaries formed an urban gradient, related to vegetation and impervious surface cover (Table 1). Vegetation cover ranged from 22% to 83% and impervious surface cover from 13% to 77% (Table 1, Ramírez et al., 2014).

2.2 | Experimental design

At each tributary, we selected three pools as replicates to characterize spatial variation in the stream and placed six leaf bags in each. Leaf bags were made with coarse mesh (pore size: 1.5 × 1.5 cm) and the leaf material consisted of 5 g of *Ficus longifolia* (Moraceae). Newly fallen leaves were collected from the ground and dried for 3 days at room temperature in the laboratory. The experiment lasted 44 days, allowing sufficient time for macroinvertebrate colonization and leaf breakdown. A leaf bag was randomly collected from each pool and stream at days 2, 4, 8, 16, 32, and 44. To control for potential leaf loss during the fieldwork manipulation, additional leaf bags were taken to the stream, but not placed. We returned the bags to the laboratory, weighed, and corrected mass loss for each collection sampling. Leaf bags were collected with a hand net (mesh 250 µm) to capture any leaf fragment or macroinvertebrates dislodged while sampling. All material was placed in individually labeled plastic bags, transported to the laboratory, and processed within a few hours after collection.

In the laboratory, leaf bags were gently rinsed with distilled water onto a 250-µm-mesh sieve to remove sediments and separate macroinvertebrates. Leaves were oven-dried at 70°C for 24 hr and weighed. A 1 g subsample was ashed at 500°C for 1 hr to estimate ash-free dry mass (AFDM). Macroinvertebrates were separated from the leaves, preserved in 96% ethanol, and labeled according to each sampling date. All insect and gastropod samples were identified to genus level, with the exception of Chironomidae which were only identified to subfamily or tribe. Other non-insect macroinvertebrates (e.g., Oligochaeta, Hirudinea, Platyhelminthes) were not identified further. Functional feeding groups were assigned using available literature (Merritt, Cummins & Berg, 2008; Ramírez & Gutiérrez-Fonseca, 2014). Abundance, taxonomic richness, and functional feeding groups of macroinvertebrates found in the leaf bags were expressed per g of AFDM remaining, and average numbers per stream (i.e., including all sampling dates) were used in analyses.

2.3 | Statistical analyses

Decomposition rates (per day) were calculated using the exponential decay model: $M_t = M_o e^{-kt}$ where M_t is the final dry mass and M_o is the initial dry mass. Decay rate coefficients (expressed as *k*) were calculated for each stream as the slope of the line between AFDM remaining percentages (log transformed) and time (days). Differences in *k* between streams were determined using analysis of variance (ANOVA), followed by a Tukey's test to compare the slopes. Linear regression analyses were used to assess relationships between vegetation cover and impervious surface and breakdown rates. Because the correlation between vegetation cover and impervious surface was 0.98, we used impervious surface in our linear regression analyses to determine the relationship with breakdown rates.

We also evaluated the relationship between decomposition rates and macroinvertebrate functional diversity using a second-order polynomial regression, to determine how functional heterogeneity influenced the processing of organic matter in our urban watershed. Functional diversity was estimated by calculating the exponential Shannon index (henceforth Exp(Shannon)) of the mean abundance of functional feeding groups for each stream. We used the number of functional groups as equivalent to the number of taxa, and the mean number of genera that belong to a feeding group as equivalent to the abundance (e.g., Angeler, Allen & Johnson, 2013; Angeler, Baho, Allen & Johnson, 2015). Exp(Shannon) is a standard diversity measure that can be used when community sizes are unequal (Jost, 2007). This metric is equally sensitive to abundant and rare functional groups, because functional groups are weighted by their proportional abundance. All the statistical analyses were run using R project (R Development Core Team, 2019, version 3.5.3).

3 | RESULTS

3.1 | Leaf litter decomposition

There was a high average percent mass loss during the first 8 days of decomposition, ranging from 10% to 17% (Figure 1). Leaf mass continued to decrease until the final date (day 44), when average mass remaining ranged from 21% to 73% depending on the stream (Figure 1). Leaf breakdown was appreciably faster in less urbanized

TABLE 1 Selected study streams, tributaries of the Río Piedras watershed, San Juan, Puerto Rico. Streams are ordered from low to high urban cover. Land use information from Ramírez et al. (2014). Additional information on water physical and chemical characteristics can be found in Ramírez et al. (2014)

Stream	Coordinates	Elevation (masl)	Watershed Area (km^2)	Vegetation cover (%)	Impervious surface (%)
Quebradas Las Curias	18°20′35.03″N, 66° 3′27.88″W	87.80 m	4.11	83.07	12.90
Montehiedra	18°20′42.69″N, 66° 4′6.12″W	63.10 m	3.83	61.69	38.20
Correo de Cupey	18°22′44.30″N, 66° 3′9.22″W	20.60 m	1.68	41.93	58.02
Río Piedras	18°23′43.38″N, 66° 3′8.69″W	19.40 m	0.19	51.41	48.50
Las Lomas	18°23′46.34″N, 66° 5′7.76″W	14.30 m	7.93	33.91	65.94
San Patricio	18°25′5.23″N, 66° 5′49.29″W	2.30 m	3.16	22.76	77.15

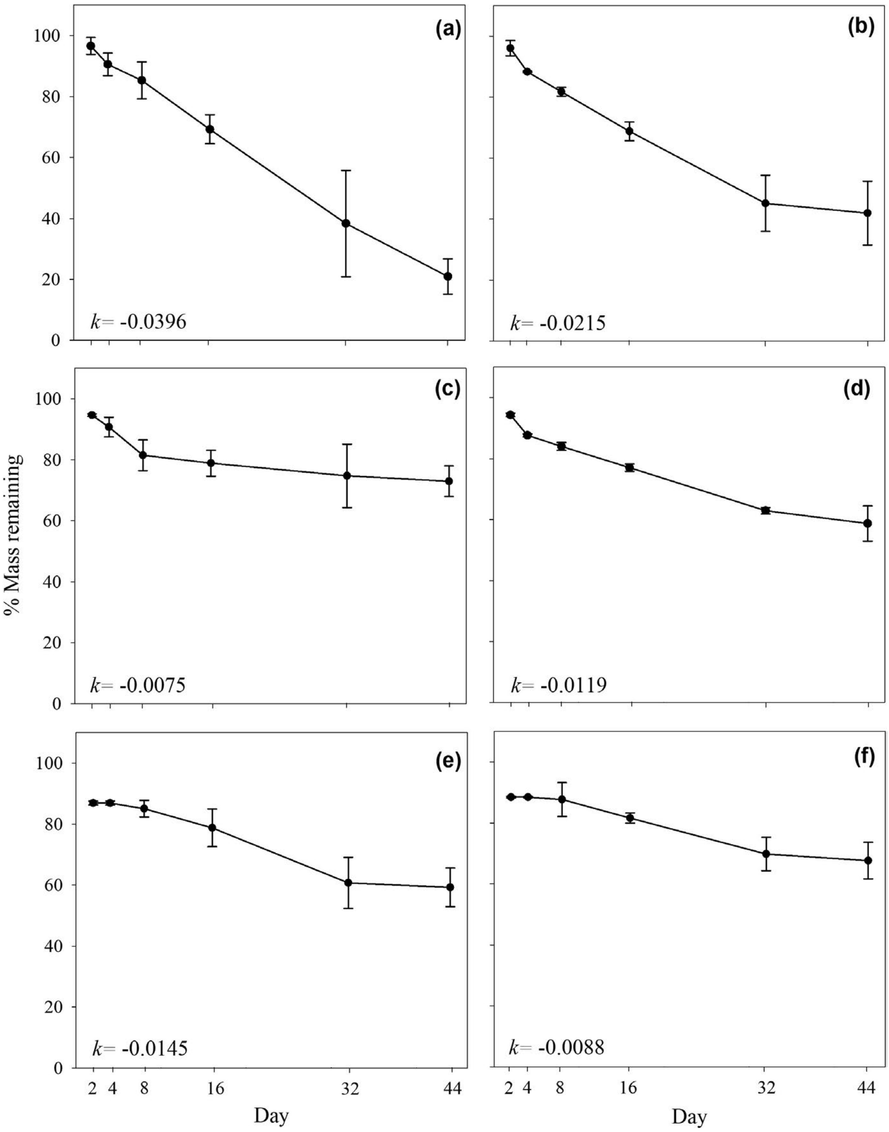

FIGURE 1 Percent mass remaining in leaf packs in the six study streams along the Río Piedras watershed. Streams are ordered from low to high urban cover. Bars represent ± *SD* (*n* = 3). (a) Quebrada Las Curias, (b) Montehiedra, (c) Correo de Cupey, (d) Río Piedras, (e) Las Lomas, (f) San Patricio

streams (i.e., at Quebrada Las Curias only 21% mass remained by day 44). In contrast, leaf mass loss in heavily urbanized streams was slow and by day 44 some had up to 73% of their leaf mass still remaining (Figure 1). Similarly, leaf breakdown rates varied among streams, and rates were fast in less urban streams (range 0.021–0.039/day) and more than double the rates from the most urban streams (all <0.015; Table 2). Decomposition rates were significantly different among streams, but mostly the result of the two least urbanized sites (Quebrada Las Curias and Montehiedra) having faster rates than the remaining streams (ANOVA, $F = 6.048$, $p = 0.005$). Tukey's post hoc test showed that Quebrada Las Curias had significantly faster decomposition rates relative to all other streams (Figure 2).

Leaf litter breakdown rates were strongly and negatively correlated with percent impervious surface cover in the subwatershed ($R = 0.81$, $p = 0.01$, Figure 3). Conversely, breakdown rates were positively correlated with percent vegetation cover in the subwatershed, which was a mixture of riparian strips and areas covered by scattered trees ($R = 0.78$, $p = 0.02$).

3.2 | Macroinvertebrate assemblages

Macroinvertebrate richness and abundance in the two least urbanized streams were dominated by insects (>80% of the total; Figure 4). In contrast, non-insect macroinvertebrates were the dominant group in all other streams, with the exception of abundance at Las Lomas, where the proportion was more even between the two types of invertebrate groups (Figure 4).

Comparison of common taxa showed that 11 groups accounted for more than 90% of total macroinvertebrate abundance (Table 3). Less urbanized streams had a high abundance of insect macroinvertebrates and high overall diversity of taxa, including *Phylloicus pulchrus* (Trichoptera: Calamoceratidae), *Neohagenulus julio* (Ephemeroptera: Leptophlebiidae), and Chironomini (Diptera: Chironomidae). More urbanized streams had high abundance of non-insect macroinvertebrates with representatives of Gastropoda of the genus *Tarebia* (Thiaridae) and the family Hydrobiidae, as well as leeches (Hirudinea).

Mean macroinvertebrate richness ranged from 2.44 taxa per gram of AFDM in the least urbanized stream to 1.71 taxa at the

TABLE 2 Leaf litter decomposition rates (*k*) and correlation coefficients (R^2) and *p*-values for the relation between leaf mass remaining and days of the experiment, in six tributaries of the Río Piedras watershed, Puerto Rico. Streams are ordered from low to high urban cover

Stream	Decomposition rates (*k*)	Standard deviation (3 pools per stream)	Correlation coefficients (R^2)	*p*
Quebrada Las Curias	−0.0396	0.0189	0.9971	<0.001
Montehiedra	−0.0215	0.0061	0.9526	<0.001
Correo de Cupey	−0.0075	0.0017	0.7772	<0.001
Río Piedras	−0.0119	0.0015	0.9616	<0.001
Las Lomas	−0.0145	0.0047	0.9572	<0.001
San Patricio	−0.0088	0.0022	0.9684	<0.001

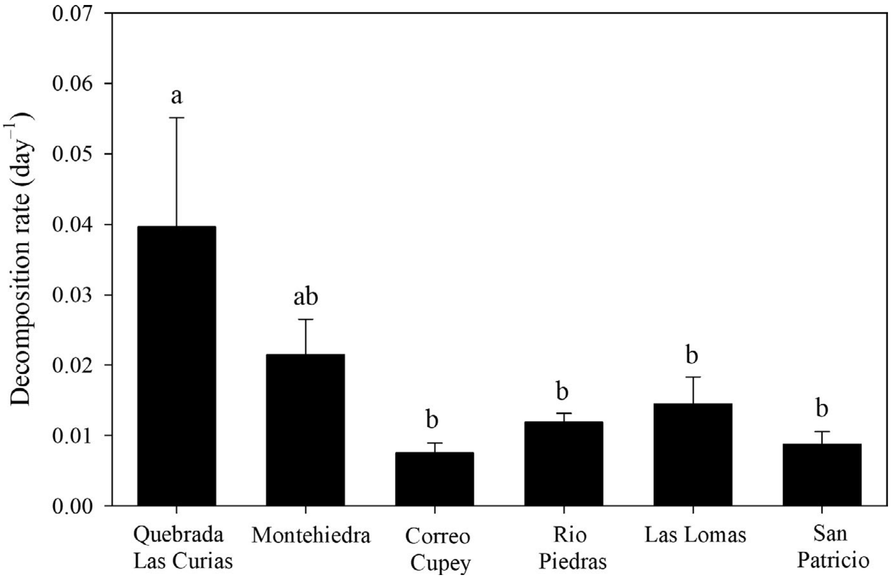

FIGURE 2 Average decomposition rates in each stream. Different letters indicate significantly different rates of decomposition (ANOVA, $F = 6.048$, $p = 0.005$)

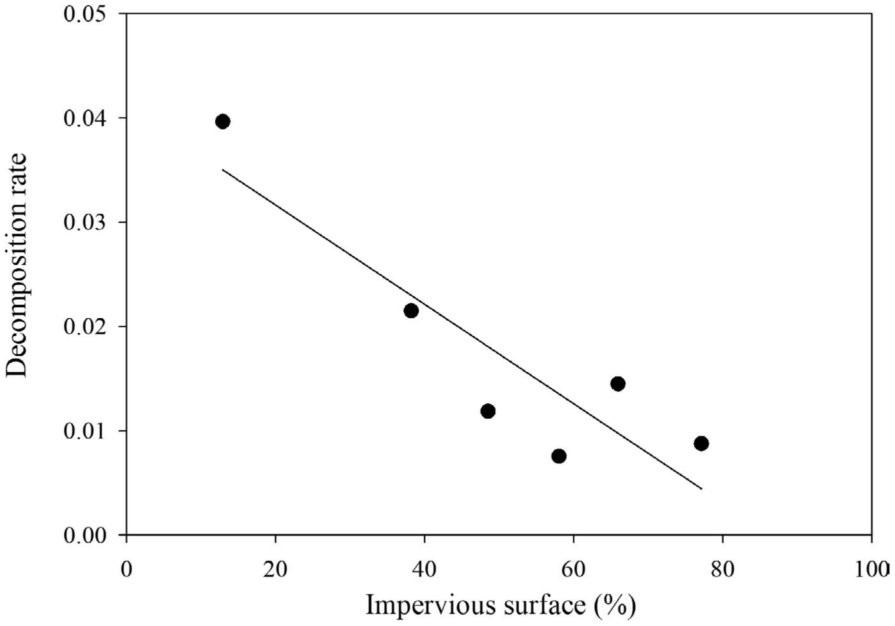

FIGURE 3 Relationship between breakdown rate (*k*) and percent impervious surface area cover in the subwatershed

most urbanized, with intermediate streams having as few as 0.67 taxa per gram of AFDM (Figure 5a). Although mean richness was slightly greater in the least urbanized stream, it did not differ significantly from other streams (ANOVA, $F = 2.05$, $p > 0.05$). Mean macroinvertebrate abundance was similar across all streams, except for the most urbanized stream (ANOVA, $F = 5.226$, $p = 0.001$).

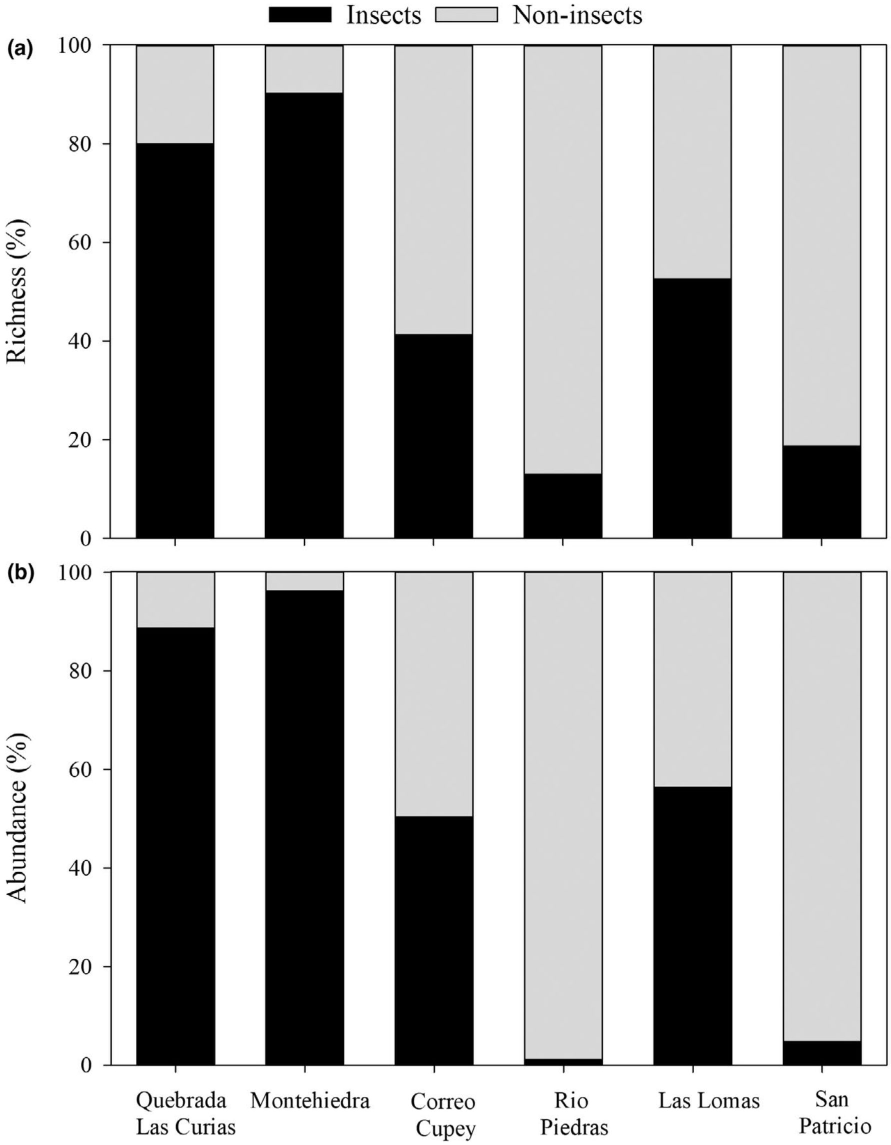

FIGURE 4 Proportions of macroinvertebrate taxa richness (a) and abundance of individuals per taxa (b) of insects vs. non-insects at each stream site along the Río Piedras watershed. Values represent the average for all sampling dates per stream

In this stream (San Patricio), macroinvertebrate abundance was 47.34 individuals per gram AFDM, which is ~4 times higher than the average for all other streams (range 4.70–18.42 individuals, Figure 5b).

Functional feeding group analysis showed that the least urbanized stream had higher functional diversity, with a more heterogeneous representation of functional groups relative to the remaining streams, which were mostly dominated by a single group (e.g., predators or grazers; Figure 6). Shredders were present only in the least urbanized streams and accounted for 55.91% and 1.35% of all FFG abundance in Quebrada Las Curias and Montehiedra, respectively (Figure 6).

The relationship between leaf litter decomposition rates and functional diversity (expressed as Exp(Shannon)) was well represented by a polynomial relationship, with a positive quadratic coefficient ($R = 0.89$, $p = 0.036$, Figure 7). Lower leaf decomposition rates were observed in streams with intermediate functional diversity and moderate urbanization levels (namely Correo de Cupey, CC in Figure 7).

4 | DISCUSSION

Our study focused on assessing the effects of urbanization on stream ecosystem function, using leaf litter decomposition as our selected study process. We expected rates of decomposition to decrease as urbanization on the watershed increased. We found support for this prediction, with higher decomposition rates in less urbanized streams. It suggests that urban streams and their ecological functions might be benefitted if enough natural characteristics are maintained. Our results also revealed that as urbanization increases in our watershed, there was a loss of macroinvertebrate assemblage and functional diversity.

Urban land use affects stream ecosystems even at relatively low levels of impervious surface on the watershed. Studies along urban gradients have provided valuable insight into the dynamics of urban stream ecosystems. Most studies have found strong negative impacts on stream diversity and ecosystem function at

TABLE 3 Abundance of the 11 most common taxa in leaf bags, as percentages of total abundance per site (including all sampling dates) in the Río Piedras watershed, Puerto Rico

Order/Taxa	FFG	Quebrada Las Curias	Montehiedra	Correo de Cupey	Río Piedras	Las Lomas	San Patricio
Trichoptera							
Phylloicus pulchrus	Sh-Dt and Sc	55.91	1.35	0.00	0.00	0.00	0.00
Ephemeroptera							
Neohagenulus julio	CG,Sc	25.11	27.50	0.00	0.00	0.62	0.00
Caenis	CG	0.00	19.95	0.00	0.00	0.00	0.00
Diptera							
Chironomini	CG	0.43	31.31	49.35	0.61	19.73	4.07
Tanytarsini	CG	0.00	0.00	0.00	0.00	23.94	0.27
Odonata							
Enallagma coecum	Pr	4.09	7.67	0.12	0.24	5.11	0.14
Gastropoda							
Tarebia	Sc	11.11	2.09	0.20	1.37	4.45	46.78
Hydrobiidae	Sc	0.00	0.00	0.00	0.00	0.00	42.53
Physidae	Sc	0.46	0.66	0.83	5.88	5.41	0.28
Annelida							
Hirudinea	Pr	0.00	0.00	47.63	90.93	30.90	2.60
Oligochaeta	CG	0.00	0.36	1.32	0.68	2.76	0.27
Total		97.11	90.88	99.45	99.71	92.91	96.93

Note: The 11 taxa compromised >90% of total macroinvertebrate abundance, and most abundant taxa per stream are underlined. Functional feeding groups follow Merritt et al. (2008) and Ramírez and Gutiérrez-Fonseca (2014)
Abbreviations: CG, collector-gatherer; Pr, predator; Sc, scrapper; Sh-Dt, shredder-detritivore.

relatively low levels of urban development (Sterling, Rosemond & Wenger, 2016; Torres & Ramírez, 2014). Negative effects on biotic assemblages and diversity are evident at urban levels below 25% (King, Baker, Kazyak & Weller, 2011). Negative effects on other stream components might be evident at even lower levels of urban cover, for example, urban levels of about 5% impact stream chemistry (e.g., Ourso & Frenzel, 2003). Our findings agree with this general scenario, showing rapid decomposition rates only at the site with the lowest urban cover (<15%). However, the relationship between impervious cover on the watershed and stream function could be complex. Some studies of leaf decomposition have found non-linear relationships along the urban gradients resulting from changes in the main mechanisms acting on leaves. In southern United States, decomposition rates were fastest at intermediate levels of urbanization, with factors like stream chemistry, hydrology, and biotic assemblages playing a role at different points along the gradient (Chadwick et al., 2006).

Decomposition rates of *Ficus* leaves are often fast in streams, given that most species in this genus are relatively rich in nutrients (Ardón & Pringle, 2008). Rates measured along the Río Piedras watershed indicated a daily mass loss ranging from 1% to 4%, which is classified as fast breakdown ($k > 0.01$) according to general leaf breakdown classifications (Peterson & Cummins, 1974). However, rates were relatively slow when compared with tropical studies using other species of *Ficus*. For example, studies in rain forest streams in Costa Rica reported *Ficus insipida* to lose 5%–11% of their mass daily (Ardón & Pringle, 2008; Rosemond, Pringle, Ramírez & Paul, 2001; Stallcup, Ardón & Pringle, 2006). In our urban gradient, leaf mass remaining was 3.5 times higher in more urbanized streams relative to less urban streams, potentially due to environmental changes and the loss of sensitive taxa (e.g., shredders). Similar findings have been reported for other urban tropical streams (e.g., Martins, Melo, Gonçalves & Hamada, 2015; Silva-Junior et al., 2014; Torres & Ramírez, 2014).

Multiple biotic and abiotic factors play a role determining rates of leaf decomposition in an urban setting. The presence of detritivorous consumers, particularly specialized taxa that shred leaves, can significantly accelerate decomposition in streams. Urbanization often results in a change in macroinvertebrate assemblage composition from high diversity to simplified assemblages dominated by generalist taxa (Barnum et al., 2017; Ramírez & Gutiérrez-Fonseca, 2014). Along our study urban gradient, macroinvertebrate shredders inhabited only the least urbanized streams, and their abundance decreased as urbanization increased. Thus, the observed simplification of macroinvertebrate assemblages from diverse functional feeding groups to dominance by snails, chironomids, and leeches was related to the observed change in decomposition rates. Similarly, studies in other tropical streams have reported changes in macroinvertebrate assemblages and consequently changes in leaf decomposition rates

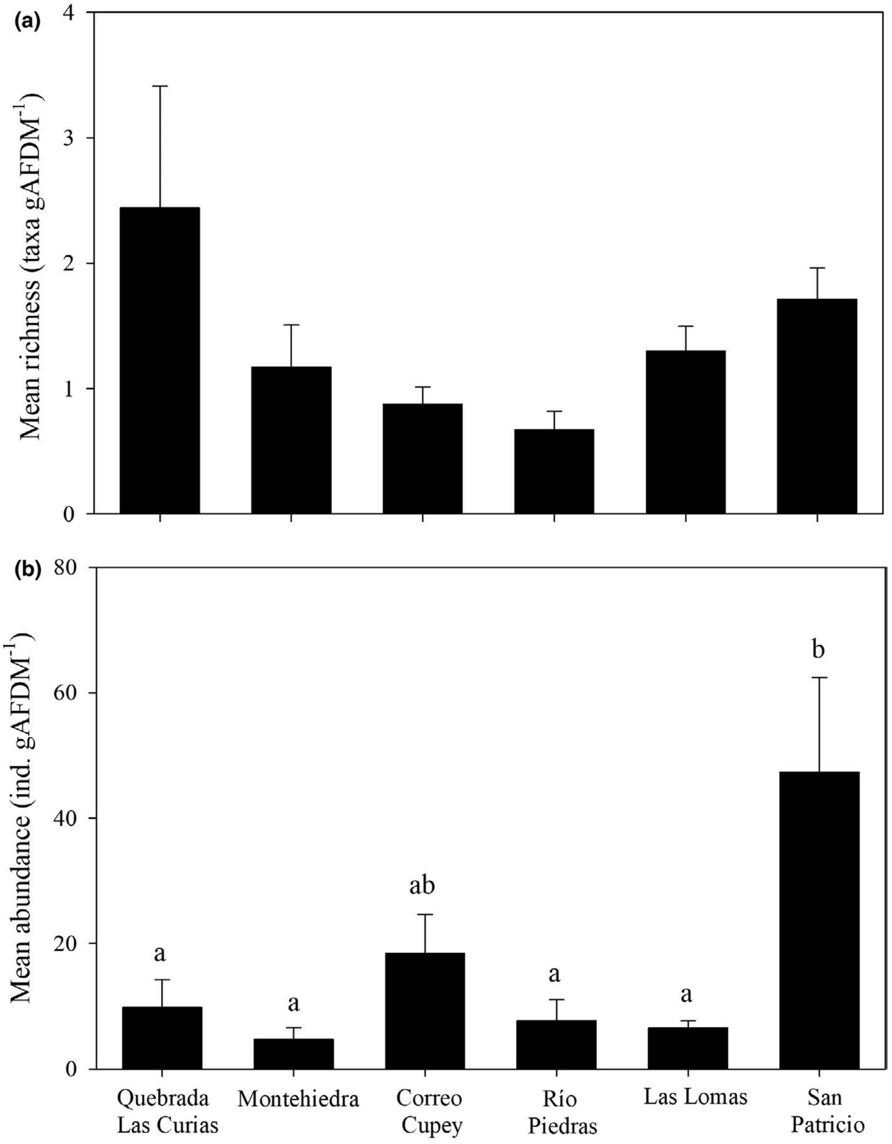

FIGURE 5 Mean macroinvertebrate taxa richness (a) and abundance of individuals (b) per gram of AFDM remaining in the study streams along the Río Piedras watershed. In (b), different letters indicate significant differences in abundance (ANOVA, $F = 5.226$, $p = 0.001$). Values based on total macroinvertebrates, using all sampling dates per stream

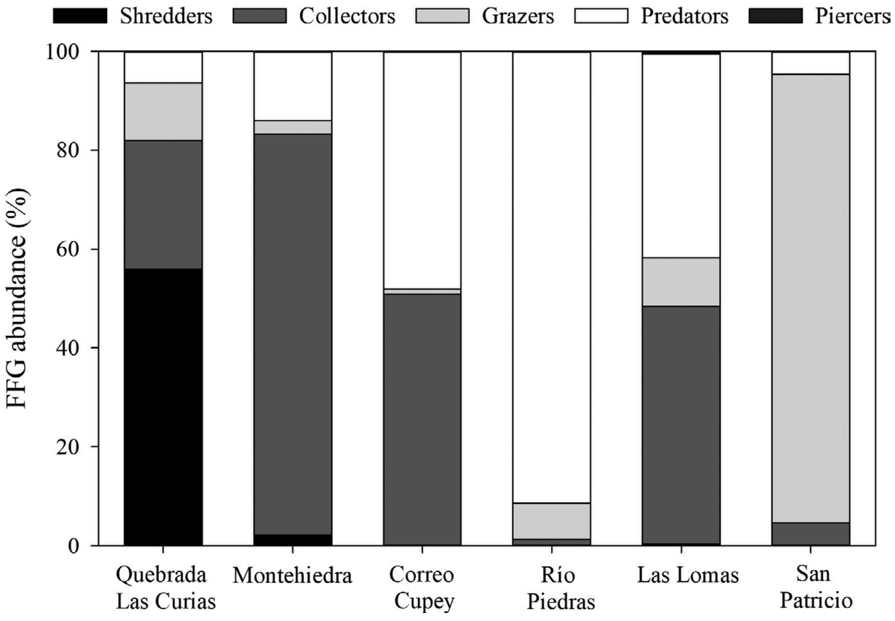

FIGURE 6 Abundance of functional feeding groups (FFGs) as percentages in each study stream along the Río Piedras watershed. *Note:* Piercers are present only in Las Lomas

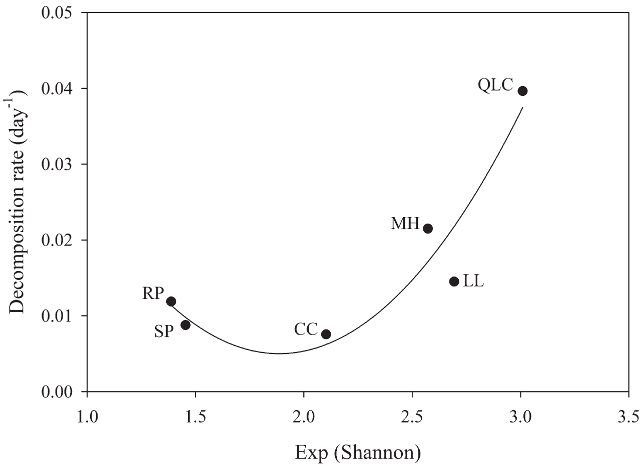

FIGURE 7 Relationship between Exp (Shannon) and leaf litter decomposition rates with polynomial regression ($R = 0.89$, $p = 0.036$)

(Martins et al., 2015). Increases in microbial activity, associated with warm water temperatures and high nutrient availability, can partially compensate for the loss of macroinvertebrate shredders with increasing urbanization (Martins et al., 2015). However, in our study streams, decomposition was much slower in urbanized streams.

The interaction of water flow and sedimentation are two abiotic factors affecting leaf decomposition, which are particularly important in urban streams. Because high water flow and flashy hydrographs cause mechanical fragmentation of leaf material, we can expect more urbanized areas to have high decomposition rates by scouring leaf material. However, intermittent and flashy regimes after storms also cause sediment deposition that can bury leaves, making them unavailable to consumers (Torres & Ramírez, 2014). Leaf pack burial reduces exposure to water flow, protecting leaves from mechanical fragmentation (Martins et al., 2015; Navel et al., 2010). In addition, leaves buried in the sediment are less accessible to consumers and could even be under low-oxygen conditions (Navel et al., 2010). In our study, we observed sediments covering some of the leaf packs in our urbanized streams. Therefore, we suggest that sediment deposition and leaf bag burial influenced the slow processing of organic matter. While we found organisms colonizing packs, they were limited to low-oxygen-tolerant species such as midge larvae (Chironomidae) (Koji et al., 2017) and annelid worms (Hirudinea and Oligochaeta).

Urban impact on functional diversity is a poorly known phenomenon that also influences ecosystem processes. Reduction in the number of functional groups, as well as changes in their abundance, can significantly alter ecosystem processes (e.g., Compin & Céréghino, 2007; Wang & Kanehl, 2003). We observed that the relationship between functional diversity and decomposition rates followed a polynomial model (Figure 7), indicating that although functional diversity was well represented in some streams, changes in specific functional groups altered the decomposition rates (Figure 5) as seen in Chadwick et al. (2006). Low rates of decomposition and diversity in urban streams were explained by the absence of shredders (Graça, 2001). Meanwhile, the low rates of decomposition and moderate representation of functional diversity in streams with intermediate urbanization can be explained by the absence of shredders and the decrease in other groups that contribute to the breaking of organic matter (e.g., grazers, Figure 5). We found high snail abundance in urbanized streams and low snail abundance in intermediate streams, and although many species of snails are classified as grazers of periphyton, some species are effective shredders of coarse detritus (Yule, Gan, Jinggut & Lee, 2015).

As urbanization continues to increase in the tropics, studies assessing its effects on ecosystem function become critical to understand impacts and develop management strategies. This work contributes to advance our knowledge of the impact of accelerated urbanization in tropical streams. Overall, we found that urbanization impacts stream ecosystem processes, in this case leaf decomposition and associated macroinvertebrate assemblages. While there are various mechanisms involved, we observed how macroinvertebrate functional diversity changed along the urban gradient and played a role influencing ecosystem function. In urbanized streams, degradation excludes the participation of macroinvertebrates that shred leaves and physical factors become an important factor controlling leaf decomposition. Efforts in urban stream conservation and restoration would benefit from improving water quality that results in high macroinvertebrate functional diversity in streams (e.g., removing sources of water pollution, restoring riparian vegetation with native tree species).

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j2p05q3 (Classen-Rodríguez, Gutiérrez-Fonseca & Ramírez, 2019).

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