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Impacts of diffuse urban stressors on stream benthic communities and ecosystem functioning: A review

Miriam Colls[1,2], Aida Viza[3], Aitziber Zufiarre[4], Alba Camacho-Santamans[3,5], Alex Laini[6], Alexia Maria González-Ferreras[7], Ana Filipa Filipe[8], Ana Victoria Pérez-Calpe[1], Anna Freixa[2,9], Anna Lupon[10], Anna C. Santamans[5], Arunava Pradhan[11,12], Carmen Espinosa[13,14], Carmen Vera-Trujillo[15], Cayetano Gutiérrez-Cánovas[16], Clara Mendoza-Lera[17], Daniel Bruno[18,19], Daniel Mercado-Bettin[2,9], Daniel Morant[5], Daniela Batista[11], David Cunillera-Montcusi[3,20], Diana Graça[11], Eduard Vico-Oton[21], Edurne Estévez[1,22], Elizabeth Leon-Palmero[23,24], Ena Lucia Suarez[25], Encarnación Fenoy[26,27], Eva Lima[17], Félix Picazo[23], Francisco J. Oficialdegui[16], François Keck[28], Giulia Gionchetta[29], Ibor Sabas[10], Ignacio Pérez-Silos[7], Ilisa Antunes[11], Inmaculada Alvarez-Manzaneda[23,24], Ioar de Guzmán[1], Isabel Fernandes[11], Janine Pereira da Silva[11], Jing Wei[30], Jorge Juan Montes-Pérez[31], José Trabulo[11], José L. J. Ledesma[32], José Maria Fernandez-Calero[3], José Pedro Ramião[11], Juan Rubio-Rios[26,27], Juan David Gonzalez-Trujillo[2,23], Laura Barral-Fraga[2,34], Laura Jiménez[18], Lidia Vendrell-Puigmitja[13], Lluís Bertrans[13], Lluís Gomez-Gener[35], Lorenzo Rovelli[17], Lukas Thuile Bistarelli[22], Marc Sanchez-Morales[36], Marco J. Cabrerizo[37,38], Maria Aranguren-Gassis[37,38], Maria Argudo[2,10], Maria J. Navarro-Ramos[16], Miren Atristain[1], Naiara Lopez-Rojo[39], Nicolás Valiente[30], Nuria Perujo[2,40], Olatz Pereda[1], Oriana Llanos-Paez[2,9], Oscar Belmar[41], Osvaldo Tascón-Peña[37,38], Pablo Rodriguez-Lozano[42], Raquel Sánchez de Pedro[43], Rebeca Arias-Real[3], Rossano Bolpagni[44], Rubén del Campo[22], Silvia Poblador[45], Simone Guareschi[16], Stephan Hilgert[46], Sofia Duarte[11], Tamara Rodriguez-Castillo[7], Teofana Chonova[28] Teresa Conejo-Orosa[31], Vanessa Céspedes[16,18], Verónica Granados[3], Víctor Osorio[10], Víctor Vazquez[47], Víctor Martin-Vélez[16] and Ferran Romero[48,*]

[1] Group of stream ecology, Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country / Euskal Herriko Unibertsitatea, UPV/EHU, Barrio Sarriena, s/n, 48940 Leioa, Spain.
[2] University of Girona, Plaça de Sant Domènec, 3, 17004 Girona, Spain.
[3] Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, Universitat de Barcelona, Barcelona, Catalonia, Spain.
[4] Área de Biodiversidad, Gestión ambiental de Navarra-Nafarroako Ingurumen kudeaketa (GAN-NIK). Padre Adoain, 219 Bajo, 31015 Pamplona-Iruñea, Navarra, Spain.
[5] Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, 46980, Paterna, Spain.
[6] Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123, Turin, Italy.
[7] IHCantabria - Instituto de Hidráulica Ambiental de la Universidad de Cantabria, 39011, Santander, Spain.
[8] Forest Research Centre, Associate Laboratory TERRA, School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-107, Lisbon, Portugal.
[9] Catalan Institute for Water Research (ICRA), Emili Grahit 101, 17003 Girona, Spain.
[10] Integrative Freshwater Ecology Group, Center for Advanced Studies of Blanes (CEAB-CSIC), Blanes, Spain.
[11] Centre of Molecular and Environmental Biology (CBMA), Department of Biology, University of Minho, Campus de Gualtar, 4710-057, Braga, Portugal.

[12] Institute of Science and Innovation for Bio-Sustainability (IB-S), University of Minho, Campus de Gualtar, 4710-057, Braga, Portugal.
[13] BETA Technological Center, University of Vic – Central University of Catalonia (UVic – UCC), 08500, Vic, Spain.
[14] Aigües de Vic S.A. (AVSA), 08500, Vic, Spain.
[15] Universidad de Málaga, Departamento de Ecología y Geología, Facultad de Ciencias. Campus Universitario de Teatinos S/N. 29071, Málaga, Spain.
[16] Estación Biológica de Doñana (EBD – CSIC). Av. Américo Vespucio, 26. Isla de la Cartuja. 41092 Sevilla, Spain.
[17] iES, RPTU University of Kaiserslautern-Landau, Forststr. 7, 76829-Landau, Germany.
[18] Pyrenean Institute of Ecology (IPE-CSIC), Avenida Montañana, 50820 Zaragoza, Spain.
[19] Department of Applied Biology, Miguel Hernández University, 03202, Elche, Spain .
[20] WasserCluster Lunz - Biologische Station GmbH. Lunz am See, Austria.
[21] Environmental Microbiology Laboratory, School of Architecture, Civil and Environmental Engineering, École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland.
[22] Department of Ecology, University of Innsbruck, Innsbruck, Austria.
[23] Department of Ecology, Faculty of Sciences, University of Granada, 18071, Granada, Spain.
[24] Institute of Water Research, University of Granada, Granada, Spain.
[25] Department F.-A. Forel for Environmental and Aquatic Sciences, University of Geneva, 1205 Geneva, Switzerland.
[26] Department of Biology and Geology, University of Almería, Almería, Spain.
[27] Andalusian Center for Evaluation and Monitoring Global Change (CAESCG), Almería, Spain.
[28] Eawag: Swiss Federal Institute of Aquatic Science and Technology, Department of Aquatic Ecology, Überlandstrasse 133, 8600 Dübendorf, Switzerland.
[29] Eawag, Swiss Federal Institute for Aquatic Science and Technology, Department of Surface Waters-Research and Management, 6047 Kastanienbaum, Switzerland.
[30] Centre for Biogeochemistry in the Anthropocene, Department of Biosciences, Section for Aquatic Biology and Toxicology, University of Oslo, 0316 Oslo, Norway.
[31] Marine Ecology and Limnology Research Group, Universidad de Málaga, 29071, Málaga, Spain.
[32] Institute of Geography and Geoecology, Karlsruhe Institute of Technology (KIT), 76131 Karlsruhe, Germany.
[33] Museo Nacional de Ciencias Naturales; Madrid, España (MNCN-CSIC).
[34] Hydrobiology Technical Unit, LDAR24, 24660, Coulounieix-Chamiers, France.
[35] Centre for Research on Ecology and Forestry Applications (CREAF), Edifici C, Campus de Bellaterra (UAB), 08193 Cerdanyola del Vallès, Barcelona, Spain.
[36] Department of Geography, Edifici B, Facultat de Filosofia i Lletres, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Bellaterra, Spain.
[37] Departamento de Ecología y Biología Animal, Facultad de Ciencias del Mar, Universidad de Vigo, Campus Lagoas Marcosende, s/n, 36310 Vigo, Spain.
[38] Centro de Investigación Mariña da Universidade de Vigo (CIM-UVigo), Illa de Toralla s/n, 36331 Vigo, Spain.
[39] Université Grenoble Alpes, Laboratoire d'Ecologie Alpine (LECA), UMR CNRS-UGA-USMB, Grenoble, France.
[40] Helmholtz Centre for Environmental Research (UFZ), Magdeburg, Germany.
[41] Marine and Continental Waters Program, Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Sant Carles de la Ràpita, Catalonia, Spain.
[42] Department of Geography, Universitat de les Illes Balears, 07122 Palma, Spain.
[43] Universidad de Málaga, Departamento de Botanica y Fisiologia Vegetal, Facultad de Ciencias. Campus Universitario de Teatinos S/N. 29071, Málaga, Spain
[44] Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, 43124 Parma, Italy
[45] Plants and Ecosystems (PLECO), Biology Department, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium
[46] Institute for Water and River Basin Management, Department of Aquatic Environmental Engineering, Karls-

ruhe Institute of Technology, Karlsruhe, Germany.
[47] Department of Research and Development, Coccosphere Environmental Analysis, C/Cruz 39, 29120 Alhaurín el Grande, Málaga, Spain
[48] Plant-Soil Interactions group, Agroscope, 8046 Zurich, Switzerland

* Corresponding author: ferran.romero@gmail.com

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ABSTRACT

Impacts of diffuse urban stressors on stream benthic communities and ecosystem functioning: A review

Catchment urbanisation results in urban streams being exposed to a multitude of stressors. Notably, stressors originating from diffuse sources have received less attention than stressors originating from point sources. Here, advances related to diffuse urban stressors and their consequences for stream benthic communities are summarised by reviewing 92 articles. Based on the search criteria, the number of articles dealing with diffuse urban stressors in streams has been increasing, and most of them focused on North America, Europe, and China. Land use was the most common measure used to characterize diffuse stressor sources in urban streams (70.7 % of the articles characterised land use), and chemical stressors (inorganic nutrients, xenobiotics, metals, and water properties, including pH and conductivity) were more frequently reported than physical or biological stressors. A total of 53.3 % of the articles addressed the impact of urban stressors on macroinvertebrates, while 35.9 % focused on bacteria, 9.8 % on fungi, and 8.7 % on algae. Regarding ecosystem functions, almost half of the articles (43.5 %) addressed changes in community dynamics, 40.3 % addressed organic matter decomposition, and 33.9 % addressed nutrient cycling. When comparing urban and non-urban streams, the reviewed studies suggest that urbanisation negatively impacts the diversity of benthic organisms, leading to shifts in community composition. These changes imply functional degradation of streams. The results of the present review summarise the knowledge gained to date and identify its main gaps to help improve our understanding of urban streams.

Key words: Anthropocene, community structure, functioning, freshwater ecosystems, urban streams, urbanization

RESUMEN

Impactos de los estresores urbanos de origen difuso en las comunidades bentónicas fluviales y el funcionamiento ecosistémico: una revisión

La urbanización de las cuencas expone a los arroyos urbanos a multitud de factores de estrés. Destacan aquellos que tienen su origen en fuentes difusas, los cuales han recibido menos atención que aquellos estresores procedentes de fuentes puntuales. Este estudio resume los avances relacionados con los estresores urbanos difusos y sus consecuencias para las comunidades bentónicas fluviales, a partir de la revisión de 92 artículos. En base a los criterios de búsqueda, el número de artículos que tratan sobre estresores urbanos difusos en arroyos ha ido en aumento, la mayoría de ellos centrados en América del Norte, Europa y China. Los usos del suelo fueron la variable más utilizada para caracterizar las fuentes difusas de estrés (el 70.7 % de los artículos caracterizó los usos del suelo), y los factores de estrés químico (nutrientes inorgánicos o propiedades del agua, como pH o conductividad) se mencionaron con más frecuencia que los factores de estrés físico o biológico. El 53.3 % de los trabajos abordaron el impacto de los estresores urbanos difusos sobre los macroinvertebrados, mientras que el 35.9 % se centraron en bacterias, el 9.8 % en hongos y el 8.7 % en algas. En cuanto al funcionamiento de los ecosistemas, prácticamente la mitad de los trabajos (43.5 %) analizó cambios en la dinámica de las comunidades, el 40.3 % en la descomposición de materia orgánica y el 33.9 % en los ciclos de los nutrientes. Al comparar los arroyos urbanos y no urbanos, los trabajos revisados sugieren que la urbanización afecta negativamente a la diversidad de organismos bentónicos, provocando cambios en la composición de la comunidad. Estos cambios implican la degradación funcional de los arroyos. Los resultados de la presente revisión resumen los conocimientos adquiridos hasta hoy e identifican sus principales carencias a fin de ayudar a mejorar nuestra comprensión de los arroyos urbanos.

Palabras clave: *Antropoceno, estructura de la comunidad, funcionamiento, ecosistemas de agua dulce, arroyos urbanos, urbanización*

INTRODUCTION

Streams have historically provided essential services to humanity thus favouring the establishment of human settlements close to them (Haines-Young & Potschin, 2010). Currently, stream ecosystem services remain essential to human well-being, as they are crucial for water and food provisioning, among others services (Palmer et al., 2009). Many urban areas are thus situated near or around streams (*urban streams*), playing an important role in the dynamics of urban development. The tight connection between stream ecosystems, and the landscape and the growing urbanisation within basins, have led to an increase in the ecological impacts faced by urban streams (Schmutz & Sendzimir, 2018), making them especially vulnerable to global change (Palmer et al., 2008; Walsh et al., 2005).

A major factor driving global change is human population growth and the resulting increased demand for natural resources (Grimm et al., 2008). In addition, human populations are progressively tending to concentrate in urban areas. Whereas in 1900, only 10 % of the world's population lived in cities, the latest United Nations (UN) assessment increased this figure to 55 % of the world's population (UN, 2018). Additionally, greater economic opportunities near urban areas compared to rural areas are promoting migrations that are expected to push the urban population to 68 % by 2050 (United Nations, 2018). Urban areas and their inhabitants exert great pressure on urban streams, acting as *stressor sources*. These include alterations in the riparian zone (e.g., loss of riparian integrity) and the watershed (e.g., impermeabilisation), which act as sources of urban stressors (e.g., heavy metals, inorganic nutrients), ultimately impacting both the structure and functioning of stream ecosystems (i.e., causing *ecological effects*; Fig. 1) (Wenger et al., 2009). Urban stressors and their ecological effects are collectively known as *urban stream syndrome* (Walsh et al., 2005).

From the management perspective, regulatory agencies identify two main stressor sources: point and diffuse sources (European Commission (EC), 2000). Factories, wastewater discharge from treatment plants, or untreated sewage are

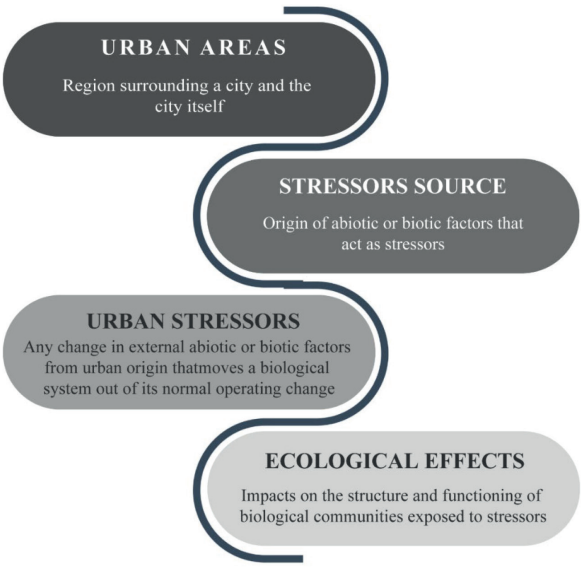

Figure 1. Conceptual framework of the interaction between urban areas and stream ecosystems. *Modelo conceptual de la interacción entre áreas urbanas y ecosistemas fluviales.*

common point sources of stressors, as they show a single identifiable origin (e.g., a pipe). Conversely, diffuse sources lack a single origin of stress, displaying scattered origins, resulting in the release of a mixture of stressors from multiple sources. The latter is the case in urban areas where for instance, the pavement does not allow water to soak into the ground, which increases the volume and velocity of runoff water and washes organic and inorganic substances into streams (Ellis & Mitchell, 2006). Due to their traceable origin, the effects of point-source stressors on stream ecosystems have been widely investigated (Pereda et al., 2019; Solagaistua et al., 2018; review: Carey & Migliaccio, 2009), whereas diffuse sources have been less researched. Hence, there is a need to broaden our knowledge about diffuse-source stressor effects on fluvial ecosystems, and this requires a review of the knowledge acquired thus far to identify the knowledge gaps and main challenges.

Urban stressors from diffuse origins ultimately reach and have an impact on the myriad of micro- and macroorganisms inhabiting urban streams. Since flow direction is the stream driv-

ing force (Reynolds et al., 1991), the growth and development of planktonic communities is slow, while benthic (i.e., attached) communities are dominant (Lampert & Sommer, 2007). Benthic macro- and microorganisms colonize multiple streambed surfaces worldwide. Their short life cycles allow them to quickly respond to environmental stressors (Burns & Ryder, 2001), and their distribution and abundance are closely related to the availability of habitats, connectivity, and environmental conditions (e.g., Bonada et al., 2007; Sabater et al., 2002). For instance, urban stressors usually imply reductions in biodiversity and the consequent biotic homogenization of benthic macroinvertebrates, bacteria, and algae (Busse et al., 2006; Cuffney et al., 2010; McKinney, 2006). At the functional level, benthic organisms play a key role in the processing of organic matter and substantially contribute to nutrient processing and retention, providing energy to higher trophic levels (Battin et al., 2016; Wallace & Webster, 1996). Stream biota homogenization produced by urban stressors threatens the proper functioning of stream ecosystems, affecting associated ecosystem services such as temperature regulation or food and water supply (Thorp et al., 2010). Declining stream flows and the increasing presence of pollutants in stream water due to growing urban pressures are promoting urban stream degradation, compromising their capacity to supply ecosystem services. Given their dominance and major role in stream ecosystems, benthic organisms may be a key monitoring tool to forecast global change risks to stream ecosystems flowing through urban areas.

The purpose of this review is to provide an up-to-date and global assessment of the effects of stressors from urban diffuse-source origins on stream benthic organisms. We specifically aim to address (i) the temporal and geographical distribution of the studies focusing on this issue to date; (ii) the stressors that are more commonly employed to characterize diffuse effects of urbanisation on benthic communities; and (iii) the structural and functional response variables most commonly employed to analyse the impacts of diffuse-source stressors of urban origin on stream communities.

MATERIALS AND METHODS

Literature search and selection

The *Web of Science* publication database was used to perform a literature review of English-language studies focusing on urban diffuse-source stressor effects on stream ecosystems published between 2000 and 2022. The literature search in the *ISI web of knowledge* (15/07/2022) was performed by combining an integrative list of (i) terms describing diffuse urban stressor impacts, (ii) the main biological groups of benthic organisms, and (iii) the most relevant stream ecosystem functions (search code: Table S1, Supplementary material, available at http://www.limnetica.net/en/limnetica). Studies analysing urban point-source stressors, diffuse-source stressors of agricultural origins, and non-lotic ecosystems were excluded from the search. Studies focusing on non-benthic organisms were also excluded. Overall, a total of 299 studies were identified under the specified search terms, which were individually screened and selected only if they fit the previously mentioned criteria. This resulted in 92 studies retained as the final article selection (see Table S2, Supplementary Material, available at http://www.limnetica.net/en/limnetica).

Data extraction and analysis

A spreadsheet was created to compile the information retrieved from the publications (Table S2). First, general information about the study was retrieved, including publication year, study location (country, continent, and North–South division), sampling season (rainy, dry, or both seasons), climate (based on the Köppen (1936) classification), and experimental approach (field survey or manipulative study). Second, we retrieved information on how the stressor source was characterized: (i) land cover, (ii) riparian integrity, (iii) population density, (iv) impervious surface, and (v) others. *Land cover* is the broadest origin category and applies to the surface cover on the ground around the sampling site. *Riparian integrity* is the set of factors evaluating the quality of the interface between land and stream. *Population density* refers to the number of inhabitants per surface unit. *Im-*

pervious surfaces refer to anthropogenic features through which water cannot infiltrate the soil. Impervious surfaces are a fraction of urban land use, which also includes vegetation and soil (Lu & Weng, 2006). Finally, the *other* category included the characterization of stressor sources based on less frequently employed parameters, such as road and dwelling density. We then retrieved information about the characterization scale, that is, the spatial range at which the stressor source was quantified (i.e., basin, reach, or both scales). Finally, data about the urban stressor category were obtained. *Stressor* is defined here as the change in any external abiotic or biotic factor that moves a biological system out of its normal operating range (homeostasis). Stressors are classified here into physical, chemical, and biological stressors; this classification has previously been used in both theoretical and experimental studies (Jackson et al., 2016; Orr et al., 2022; Romero et al., 2018). *Physical stressors* included alterations in the hydrology and/or morphology of the stream channel. Hydrological alterations were related to discharge and flow dynamics changes, including increased turbidity. Morphological alterations were associated with streambed and bank modifications (Elosegi et al., 2019). *Chemical stressors* mainly referred to increases in the concentration of xenobiotics, nutrients or metals in water or sediment (Booth et al., 2016; Paul & Meyer, 2001), as well as alterations in other parameters related to water chemistry (e.g., pH and conductivity). *Biological stressors* included invasive species as well as pathogenic microorganisms and their toxins (Havel et al., 2015). The observed ecological effects of urban stressors on structural and functional variables were gathered from the reviewed articles. Structural variables referred here to the characteristics of a biological community as measured by any metric of taxa composition, diversity and/or abundance via molecular techniques or direct observation. Here, functional variables were defined as ecosystem processes or their proxies. When structure was analysed, information about the target group (i.e., taxonomy of organisms that were the focus of the study) and the identification method (i.e., visual or molecular) was extracted. Visual methods included those that, with the aid of a microscope or the naked eye, assigned taxonomy based on morphological traits. Molecular methods were those where taxonomy was assigned based on genetic analyses, either by gene sequencing or by community fingerprinting. In the studies where the functional response was analysed, information about target function was obtained and classified into five categories based on von Schiller et al. (2017): organic matter (OM) decomposition, nutrient cycling, metabolism, pollutant dynamics, and community dynamics. OM decomposition included the decomposition of both coarse and fine organic particles, as well as the uptake and degradation of dissolved OM (e.g., humic substances, proteins, and sugars), as well as exoenzymatic activities. Nutrient cycling included the uptake of nutrients and the processes within the cycle of a particular nutrient (e.g., nitrification, denitrification, N fixation). Metabolism included primary production and respiration rates. Pollutant dynamics included the capacity of stream organisms to attenuate dissolved pollutants such as pharmaceuticals and metals, while community dynamics included the movement, drift, colonization, and related physiological processes of organisms. More details about functional classification are available in von Schiller et al. (2017). We added an additional category, methanogenesis. Methods for measuring functioning were then classified depending on whether a given function was directly measured (e.g., gas exchange rate, biomass accumulation, degradation of a pollutant) or inferred from the abundance/presence of a gene or enzyme (e.g., by quantitative PCR).

RESULTS

Temporal and geographic distribution of studies

The number of studies addressing diffuse urban stressor effects has increased in recent years (Fig. 2a). The number of publications per year was low from 2000 until 2013 (n = 26), representing 28.3 % of the published studies. This value increased between 2014 and 2022 (n = 66), with a maximum of 10 studies published in 2018 and 2021, comprising 71.7 % of all the publications included in this review. Among the selected publi-

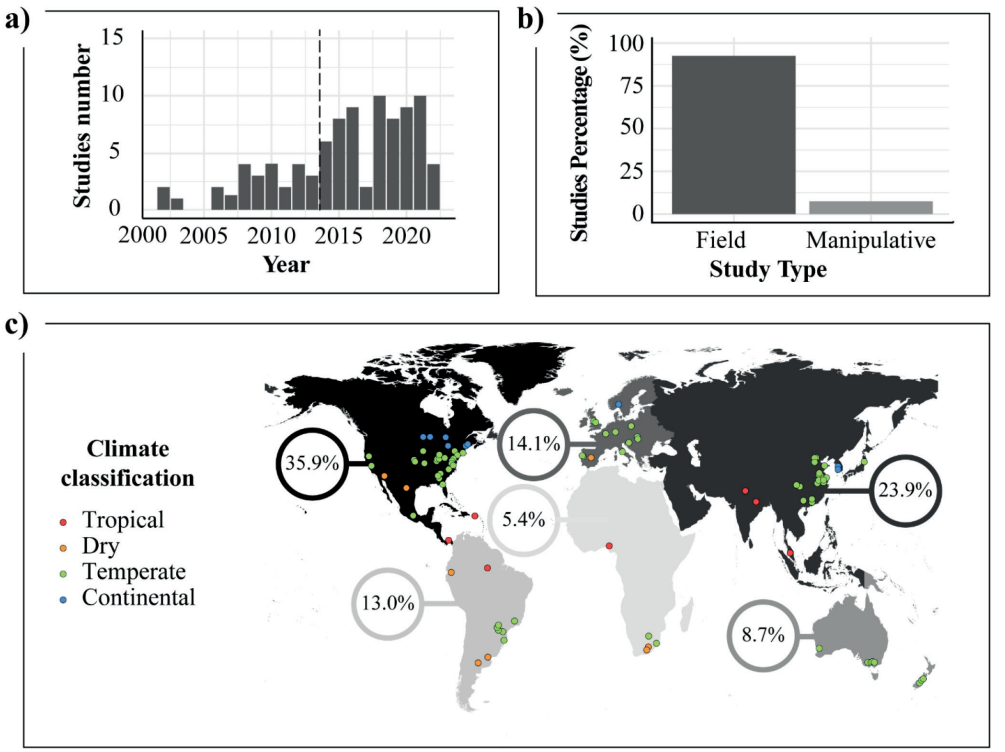

Figure 2. Temporal and spatial distribution of the studies included in this review. a) Number of publications per year in the period 2000–2022. The vertical dashed line indicates the trend change, b) experimental approach, and c) continental distribution of studies. *Distribución espaciotemporal de los estudios incluidos en esta revisión. a) Número de publicaciones anuales en el período 2000–2022. La línea vertical indica el cambio de tendencia, b) aproximación experimental, y c) distribución continental de los estudios.*

cations (n = 92), field surveys represented 92.4 % (n = 85), while only 7.6 % (n = 7) followed manipulative approaches (Fig. 2b). 35.9 % of studies were carried out in North America (n = 33), followed by Asia and Europe, with 23.9 % (n = 22) and 14.1 % (n = 13), respectively (Fig. 2c). Few studies were conducted in South America (13.0 %; n = 12), Oceania (8.7 %; n = 8), and Africa (5.4 %; n = 5) (Fig. 2c). One study was simultaneously performed and included in both North America and South America. Among the studies performed in North America, 81.8 % were conducted in the United States (n = 27). Similarly, 58.3 % of the studies carried out in South America were performed in Brazil (n = 7), and China included 72.7 % of the studies performed in Asia (n = 16). 73.9 % were performed in the Northern Hemisphere (n = 68), and 27.2 % were performed in the Southern Hemisphere (n = 25). Focusing on the North–South division, 57.6 % of reviewed studies were conducted in the Global North (n = 53), whereas 43.5 % were conducted in the Global South (n = 40).

Temperate climate dominated among field studies (82.4 %; n = 70) (Fig. 2c). Studies performed in continental, tropical, and dry climates were less frequent, representing 11.8 % (n = 10), 9.4 % (n = 8), and 8.2 % (n = 7), respectively (Fig. 2c). One study was simultaneously performed and considered in four climatic regions: tropical, dry, temperate, and continental. Finally, 67.4 % of the studies did not consider seasonality as a factor (n = 62). Among them, 39.1 % collected samples during the dry season (n = 36), 20.7 % during the rainy season (n = 19), and in 7.6 % of the cases, the sampling date was not reported (n = 7). Among those that sampled in both seasons (n = 30), 70.0 % considered seasonality as a factor in statistical analyses (n = 21), and 30.0 % did not (n = 9).

Diffuse urban stressor characterization

Among the studies describing the source of diffuse urban stressors (81.5 %; n = 75) (Fig. 3a), we found land cover was the factor most commonly identified to characterize stressor sources (70.7 %; n = 65), followed by riparian integrity (35.9 %; n = 33) and impervious surface (12.0 %; n = 11). 5.4 % (n = 5) studies used population density to characterize stressors sources and 10.9 % used other classification categories (Fig. 3b). Since some studies used more than one factor to characterise the source of diffuse urban stressors, the sum of all source categories does not equal 100 %. We also found that 53.3 % of studies (n = 49) characterised stressor sources at the basin scale, 8.7 % (n = 8) at the reach scale, and 19.6 % (n = 18) at both scales (Fig. 3a).

We found that 90.2 % (n = 83) of the studies addressed at least one stressor category (i.e.,

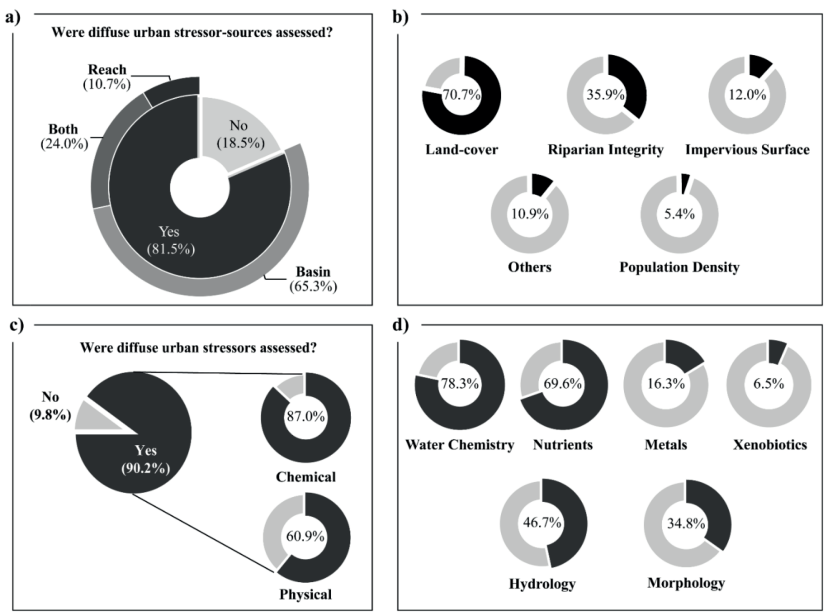

Figure 3. Distribution of reviewed studies based on stressor source (a, b) and category (c, d). *Distribución de los estudios revisados en base a la fuente (a, b) y categoría (c, d) de estresor.*

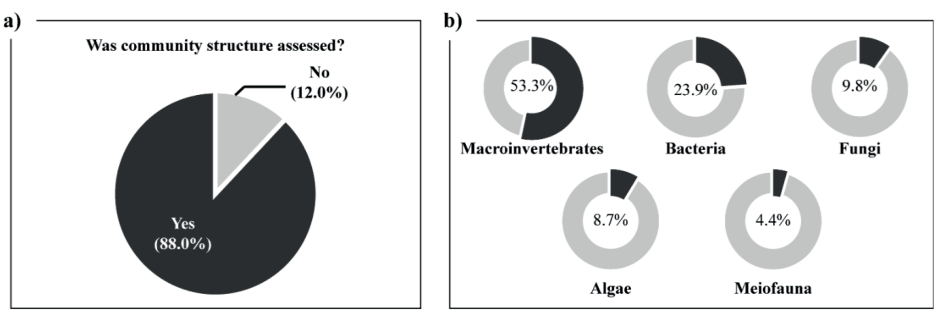

Figure 4. Distribution of reviewed studies based on taxonomic groups addressed. *Distribución de los estudios revisados en base al grupo taxonómico empleado.*

chemical, physical, or biological stressors). The remaining 9.8 % (n = 9) studies characterized only the stressor source. Specifically, 87.0 % (n = 80) of studies analysed chemical stressors, and 60.9 % (n = 56) analysed physical stressors (Fig. 3c). Regarding chemical stressors, 78.3 % (n = 72) analysed water chemical properties (e.g., pH, conductivity), 69.6 % (n = 64) nutrients, 16.3 % (n =15) metals, and 6.5 % (n = 6) xenobiotics. Regarding physical stressors, 46.7 % of studies (n = 43) analysed hydrological alterations, while 34.8 % (n = 32) assessed morphological alterations (Fig. 3d). None of the studies in our review addressed biological stressors.

Benthic biodiversity in urban streams affected by diffuse-source stressors

Out of the 92 studies that met our selection criteria, 88.0 % (n = 81) addressed the biological response to diffuse urban stressors through the community composition of at least one biological group (Fig. 4a). Among them, 53.3 % (n = 49) studied the macroinvertebrate response, and 23.9 % (n = 22) reported the bacterial response. Diffuse urban stressor effects on fungi and algae were less frequently studied, representing 9.8 % (n = 9) and 8.7 % (n = 8), respectively. Finally, only 4.4 % (n = 4) of the studies addressed the impacts of diffuse urban stressors on meiofauna (Fig. 4b). The identification techniques used to characterise community composition were closely related to the target taxonomic group. Among studies assessing community composition, 63.0 % (n = 58) employed visual identification, and 20.7 % (n = 19) employed molecular sequencing techniques; the remaining two studies used molecular non-sequencing techniques.

Focusing on the macroinvertebrate community, we found a decrease in diversity and richness associated with urbanisation (e.g., Castro-López et al., 2019; Lemes da Silva et al., 2020). Such changes were associated with the dominance of Chironomidae, Simuliidae, and Oligochaetes-Tubificidae in urban streams (e.g., Luo et al., 2018; Malacarne et al., 2016), whereas Gastropoda, Crustacea, Ephemeroptera–Plecoptera–Trichoptera (EPT), and Odonata were decimated (e.g., Bozóki et al., 2018; Del Arco et al., 2011).

Regarding stream microorganisms, the studies included here reported that some α- and β-classes of the *Proteobacteria* phylum were favoured by diffuse chemical stressors, whereas *γ-Proteobacteria* generally decreased as the presence of diffuse chemical stressors increased (e.g., Cai et al., 2016). Fungal communities also changed from non-urban to urban streams (e.g., Bärlocher et al., 2010; Miura & Urabe, 2015), although studies suggest that substrate quality overcomes urbanisation as a driver of stream fungal communities (e.g., Imberger et al., 2008; Miura & Urabe, 2015). Fungal biomass, richness, and density are usually higher in non-urban streams than in urban streams (e.g., Bärlocher et al., 2010; Emilson et al., 2016; Paul et al., 2006). Some reviewed studies found that urban chemical stressors favour taxa within the Ascomycota phylum, such as *Eurotiomycetes* and *Agaricomycetes* (Emilson et al., 2016; Gao et al., 2022; Samson et al., 2020). Finally, studies focusing on the algal community found that these communities are sensitive to both chemical and physical stressors from urban origins, mainly because of their light dependence and low mobility (e.g., Beaulieu et al., 2014; Chen et al., 2019). The studies included here found *Gomphonema* and *Achnanthidium* to be sensitive to diffuse chemical and physical stressors, whereas *Navicula* and *Nitzschia* were generally found to be tolerant to urbanisation-related stressors (e.g., Salinas-Camarillo et al., 2021; Stenger-Kovács et al., 2020).

Ecosystem functioning in urban streams affected by diffuse-source stressors

We found that 67.4 % (n = 62) of the studies addressed at least one ecosystem function (Fig. 5a). The most frequently addressed functional category was community dynamics, followed by OM decomposition and nutrient cycling, which were reported in 29.3 % (n = 27), 27.2 % (n = 25), and 22.8 % (n = 21) of the studies, respectively. Additionally, 12.0 % (n = 11) of studies analysed metabolism, 5.4 % (n = 5) analysed pollutant dynamics, and 3.3 % (n = 3) methanogenesis (Fig. 5b).

Regarding the methodology employed to characterise ecosystem functions, we found that some studies directly measured a process or rate (e.g.,

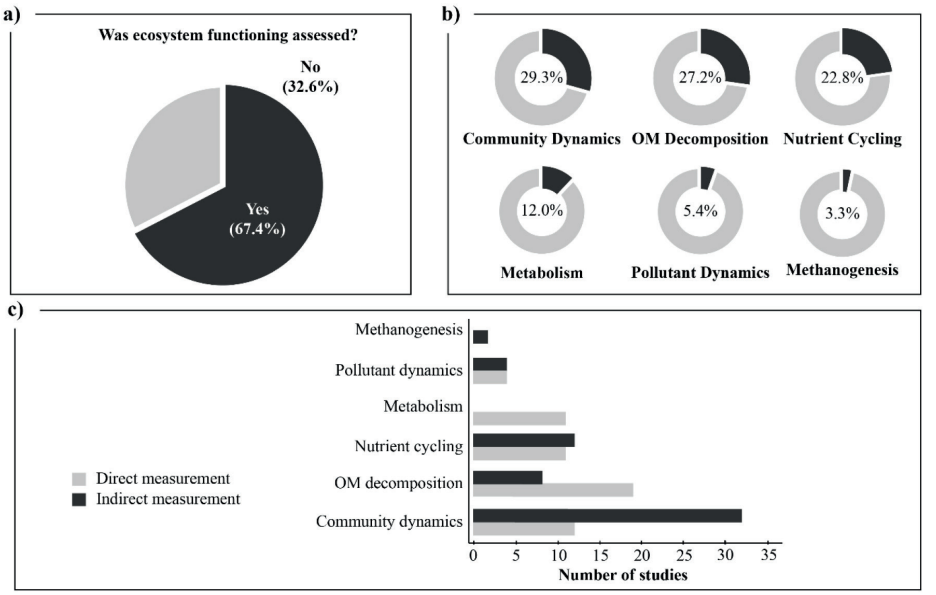

Figure 5. Distribution of reviewed studies based on ecosystem functions addressed. *Distribución de los estudios revisados en base a la función ecosistémica empleada.*

on-site OM loss), while others inferred potential function from the presence of a gene or functional group. Note that some studies addressed the same function both directly (e.g., measuring a process on-site) and indirectly (e.g., quantifying a functional gene) (Fig. 5c). Among studies analysing community dynamics (32.6 %; n = 30), most focused on consumption and related physiological processes. Functional feeding group (FFGs) was the indirect method most used to assess food ingestion mode (27.2 %; n = 25), followed by the direct measurement of secondary production (8.7 %; n = 8) and food web indirect analyses (7.6 %; n = 7). Based on FFGs, shredders decreased in urban streams, whereas gatherer-filterers, filterers, and scrappers tended to dominate (e.g., Alberts et al., 2018; Edegbene et al., 2019). Urban food webs were generally less complex, had lower trophic redundancy, and homogenized energy flow from lower to higher trophic levels (e.g., Malacarne et al., 2016; Yule et al., 2015).

OM decomposition was the second most assessed ecosystem function (27.2 %; n = 25), and it was mostly evaluated through direct measurement of coarse and fine OM decomposition (20.7 %; n = 19) but also indirectly through exoenzymatic activities under standard conditions (8.7 %; n = 8). Our review suggests that urban land use reduces leaf litter inputs and consequently OM decomposition (e.g., Emilson et al., 2016; Jung et al., 2014). The most frequently addressed nutrient cycle was that of nitrogen (e.g., denitrification, nitrification or ammonification), with 13 studies addressing at least one nitrogen-related function. Regarding the method used to measure nutrient cycling, we found that the use of indirect methods (13.0 % studies; n = 12) was preferred over direct methods (5.6 %; n = 5). For example, six studies inferred denitrification potential from the abundance of genes encoding the key enzymes, while four addressed actual denitrification rates (reduction of nitrate and/or production of its reduced chemical forms). Reviewed articles mainly suggest that urban land use favours denitrification (e.g., Newcomer et al., 2012; Perryman et al., 2011). Less frequently studied functions were metabolism (primary production and/or respiration, 13.0 %; n = 12), pollutant dynamics (5.4 %; n = 5), and methanogenesis (3.3 %; n = 3). Pollutant dynamics were mainly addressed using

indirect methods, i.e., inferring the capacity of the community to degrade pollutants from the abundance of the genes encoding enzymes involved in the degradative pathway.

DISCUSSION

Land-use changes associated with urbanisation degrade stream ecosystems and threaten the provision of services on which millions of people rely. Characterizing the impacts of urbanisation on stream ecosystems is important for the current and future management of urban streams, as the effects of climate change on stream ecosystems are expected to be influenced by the degree of anthropization within stream basins (Palmer et al., 2009). Our review of 92 studies showed that the number of scientific studies addressing the ecological effects of diffuse urban stressors on stream benthic communities has increased during the last decade. We show, however, that there is a bias towards Europe, North America, and China, as most of the studies were carried out in these regions. We found land use and riparian integrity to be the main factors used to characterize stressor sources. Chemical stressors were found to be the most frequently addressed, especially nutrients and water properties, such as pH and conductivity. Unexpectedly, none of the studies addressed biological stressors (e.g., pathogenic bacteria and their toxins). We argue that our selection criteria might have discarded papers focusing biological stressors as these are frequently associated to point (i.e., non-diffuse) stressor sources (e.g., wastewater discharge) (Kim et al., 2005). The structure of the benthic community has frequently been addressed, especially invertebrates and bacteria. Regarding ecosystem functioning, we observed that the most frequently addressed functions were community dynamics (e.g., invertebrate functional traits including feeding groups), OM decomposition, and nutrient cycling.

Global bias in research on the impacts of urban diffuse stressors on stream ecosystems

A clear bias was found towards the Northern Hemisphere, as evidenced by the large number of studies conducted in the United States, Asia, and Europe. Although the present study may be partially biased towards the Global North (because only English-language studies were selected), it seems clear that there is a knowledge gap regarding the impacts of urban areas on stream ecosystems from the Southern Hemisphere. We acknowledge here some reasons for the urgent need to include streams from the Southern Hemisphere in future studies on the impacts of urban stressors on stream ecosystems. First, water treatment technologies tend to be less developed in the Global South (Arku & Marais, 2021) and environmental protection policies tend to be based on Global North experiences, despite differences in services and resources (Fernández, 2014). Hence, it is to be expected that the impacts of diffuse urban stressors on stream ecosystems are greater in the Global South than those in the Global North. Second, air pollution is also higher in cities from the Global South; pollutants such as particulate matter, nitrogen oxide, heavy metals, and carbon monoxide are especially prevalent in the air of major Indian and Mexican cities (Akimoto, 2003). Given that atmospheric deposition is an important pathway for diffuse chemical stressors (Walsh et al., 2005), we argue that higher concentrations of air chemicals are likely to result in more degraded stream ecosystems. Second, there are approximately 35 megacities globally, with 25 of these located in the Global South. This growth trend is not likely to decrease. Three countries, India, China, and Nigeria, may be responsible for 35 % of the global population increase by 2050 (UN-Habitat, 2019). This will likely put even more pressure on streams around which such cities are growing; this is the case for the Yamuna (Delhi, India) and the Ogun (Lagos, Nigeria) stream basins (Kniveton et al., 2012). Such rapid development of cities will likely deteriorate urban environments and make urban streams especially vulnerable to climate change (Bandauko et al., 2021; Taylor & Peter, 2014). Finally, climatic differences between hemispheres increase uncertainty over potential interactions of urban stressors with climate (Kottek et al., 2006). Of the studies included in this review, 73.7 % were performed in temperate climates. However, temperate regions cover only 16.5 % of the Earth's surface, whereas dry, continental, and tropical climates are more dominant. Given the projected

increase in the population of the Global South and potential interaction with climatic (i.e., physical) stressors, we encourage the study of the effects of urbanisation in regions of the world other than those in northern latitudes.

Diffuse urban stressor characterization

The results reveal a lack of consensus on the temporal and spatial scale at which diffuse urban stressors and their sources must be characterised. The scale at which abiotic variables should be considered is generally accepted as a critical issue to produce general predictions (Chave, 2013). Accordingly, most of the studies included in this review followed a basin-scale approach. However, some studies have emphasized the high sensitivity of certain taxonomic groups (e.g., macroinvertebrates) to local-scale variables (Luo et al., 2018), suggesting that local-scale restoration has the potential to generate greater benefits for communities inhabiting urban streams than managing urban stressors at the basin scale (Gwinn et al., 2018). In line with this, Mutinova et al. (2020) found that riparian attributes explained a significant proportion of the total variation in diatom communities, indicating that riparian buffers at the local scale can provide numerous co-benefits in multifunctional urban landscapes. Nevertheless, these results are not canonical and are contradicted by other studies (Hlúbiková et al., 2014). Together with the spatial scale, the temporal scale at which urban stressors impact stream ecosystems might also be very relevant for stream communities and associated functions. However, a large fraction of the studies included here overlooked the temporal scale of diffuse urban stressors. Studies considering temporal scales suggest that annual hydrological changes due to seasonality could have potential importance in stream ecosystem responses to urban stressors (e.g., Arenas-Sánchez et al., 2021; Mutinova et al., 2020). Thus, reduced dilution capacity during the dry season results in greater impacts of chemical stressors, whereas physical stressors are the main drivers of community structure and functioning during the wet season (e.g., Arenas-Sánchez et al., 2021). A thorough understanding of the effects of seasonality on the strength of diffuse urban stressors is key to coping with extreme climatic events (e.g., floods and droughts), as well as regional climate changes brought about by global change.

Our review also points to a lack of a comprehensive characterization of streams affected by diffuse urban stressors, e.g., only six studies determined xenobiotic concentrations, and 15 measured heavy metals. Xenobiotics and heavy metals were here less frequently addressed than other chemical stressors (e.g., inorganic nutrients), yet they may have dramatic single and combined effects on freshwater ecosystems (Sabater et al., 2007), so we highlight here the need to address urban stressors other than increased nutrient concentrations in future studies. Finally, we highlight here that none of the studies included in this review addressed the impacts of biological stressors of urban origins on stream ecosystems. We acknowledge that this might be because our literature search explicitly discarded studies from point sources of stress, such as wastewater treatment plants, from which most biological stressors originate (Cai & Zhang, 2013).

Macroinvertebrates overcome microorganisms as a target group to assess diffuse urban stressor effects on stream ecosystems

Macroinvertebrates were the taxonomic group most employed to address diffuse urban stressors. This finding resembles the trend observed in a previous literature review covering the period 1988–2008 on the effects of urbanisation (including both point- and diffuse-source stressors), where authors found that the biological assemblages most frequently addressed were fish and macroinvertebrates (Wenger et al., 2009). Indeed, Wenger et al. (2009) highlighted the need for increased research on the relationship between urbanisation and the structure and function of microbial communities and their associated services. Fourteen years later, we see how the impacts of urbanisation on certain microbial groups (i.e., bacteria) are starting to be addressed, but there is still a long way to go, especially for other groups (e.g., fungi, protists). We acknowledge that the over-representation of macroinvertebrates in this review might be partially due to the fact that most studies included here addressed small

streams (e.g., tributaries of larger streams), where macroinvertebrates are known to be very diverse, and ecologically relevant (Finn et al., 2011).

Our review confirms that urban stressors impact macroinvertebrate communities, leading to stream food web simplification and size reduction (e.g., Gwinn et al., 2018; Yule et al., 2015; Zhang et al., 2010). For instance, reviewed articles show that urbanisation results in the reduction of leaf litter inputs to streams, leading to the reduction of shredder communities (Alberts et al., 2018; Carroll & Jackson, 2009; Fu et al., 2016; Lemes da Silva et al., 2020). This is consistent with the reduction in EPT, which dominate the shredding feeding mode and are particularly sensitive to chemical stressors such as pollutants (Tachet et al., 2010). Moreover, food web simplification in urban streams fits with the observed reduction in richness and diversity of Odonata (e.g., Castro-López et al., 2019; Yule et al., 2015). Conversely, urban stressors (particularly chemical stressors) led to increases in Chironomidae, Simuliidae, and Tubificidae, which are mainly gatherer-filterers, filterers, scrappers and fine sediment consumers, and stress-tolerant taxa (Tachet et al., 2010).

Despite these observed patterns, we acknowledge that most of the studies in this review were performed in temperate streams and that the impacts of urbanisation on tropical stream macroinvertebrates and their functions might differ, as these streams generally show lower availability of high-quality leaf litter, being systems where decomposition is carried out by fungi rather than macroinvertebrates (Boyero et al., 2011).

The lack of more studies analysing the effects of diffuse urban stressors on microorganisms hinders our capacity to draw any clear conclusions, but some general patterns have been observed. For instance, chemical stressors favour bacteria able to metabolize contaminants and with antibiotic resistance (W. Cai et al., 2016). Regarding algae, we call for future studies analysing the impacts of urban stressors from diffuse origins on algal groups other than diatoms. Previous studies on the impacts of urbanisation have found that green algae are benefited by moderate-to-high nutrient availability, whereas cyanobacteria blooms are often favoured by anthropogenic impacts, such as diffuse urban stressors (Necchi, 2016).

The lack of studies addressing microbial communities is surprising due to the acceptance of microorganisms as useful indicators of stream water quality (Burns & Ryder, 2001) and the increased accessibility to DNA-based approaches. We argue that the lack of studies regarding the impacts of urban diffuse stressors on stream microorganisms is certainly hindering our capacity to better understand how cities alter microbial-driven functions, such as the N cycle, stream metabolism, and methanogenesis.

Additionally, identifying microbial bioindicators of urbanisation could help improve decision-making processes and prioritization policies (Sagova-Mareckova et al., 2021). For example, microbial indicators of chemical stress (e.g., heavy metal pollution) could provide direct, valuable, and inexpensive information about urban stream ecological status (Astudillo-García et al., 2019). Similarly, microorganisms could also be useful as bioindicators of pesticide exposure; although pesticides are generally associated with agriculture, they also reach streams from urban green areas (e.g., municipal gardens and parks) (Meftaul et al., 2020). However, identifying microbial bioindicators of urban stressors will necessarily require validating that those taxa, or genes, are consistently associated with a particular aspect of water quality (e.g., heavy metals or xenobiotics) across study sites. Identifying these microbial bioindicators will therefore require a comprehensive, cross-site characterization of urban streams.

Ecosystem functioning and its relationship with biodiversity in streams affected by diffuse urban stressors

Our review demonstrated that community dynamics, OM decomposition, and nutrient cycling were the ecosystem functions most frequently reported to investigate the effects of diffuse urban stressors on stream ecosystems. Nevertheless, other important ecosystem functions have received much less attention, such as methanogenesis and xenobiotic degradation. OM degradation was generally directly measured, whereas community dynamics and nutrient cycling were generally inferred from functional traits or genes involved in nutrient

transformation pathways. That was also the case of the studies analysing pollutant dynamics; they inferred xenobiotic degradation from the abundance of genes (DNA) or transcripts (mRNA) involved in xenobiotic degradative pathways. We acknowledge here that indirect measures can provide an estimate of the potential ecosystem capacity to process chemical stressors such as nutrients or pollutants. However, we argue that direct measures of the rates at which ecosystem processes operate in urban streams are needed to obtain a reliable picture of ecosystem functioning in urban streams (Smith & Osborn, 2009).

Biodiversity has an intrinsic value per se, but if we want to offer appropriate adaptation strategies to address the anticipated risks of global change to urban stream ecosystems, we need to disentangle the effects of urbanisation on the biodiversity–ecosystem functioning (B–EF) relationship of stream ecosystems. This knowledge will allow us to identify where we should focus our management efforts and which taxonomic groups need to be prioritized to maintain adequate ecosystem functions and mitigate the effects of global change (Ranta et al., 2021). This issue was already identified as one of the major knowledge gaps in urban stream ecology thirteen years ago (Wenger et al., 2009), and we argue here that this knowledge gap has not yet been filled. Experiments conducted at small spatial scales focusing on a few taxonomic groups generally show a positive relationship between diversity and ecosystem functions, but it is unclear whether this pattern holds across multitrophic communities or larger spatial scales, especially after multifactor disturbances (e.g., urbanisation) (Srivastava & Vellend, 2005). A recent study found that factors characterizing urbanisation have a negative effect on B–EF relationships (Zúñiga-Sarango et al., 2020), but this and other studies are still limited to a few stressors (e.g., nutrients, reduced oxygen) and taxonomic groups, such as macroinvertebrates (Wiederkehr et al., 2020; Zúñiga-Sarango et al., 2020). For example, Wiederkehr et al. (2020) found that urbanisation impaired ecosystem functioning more than macroinvertebrate and algal community structure, suggesting a lack of functional redundancy in urban streams.

Finally, we highlight here the need to simultaneously address multiple stressors in urban streams. In line with this, recent studies at medium to large spatial scales have concluded that interactions among stressors drive both autotrophic and heterotrophic community composition in stream ecosystems (Birk et al., 2020; Gutiérrez-Cánovas et al., 2022). This has also been observed at the local scale using experimental microcosms (Romero et al., 2019, 2020). Mitigation measures addressing several urban stressors simultaneously could include the restoration of riparian integrity in highly channelized streams, as this would hinder the discharge of toxic chemicals into stream water while simultaneously regulating water temperature and avoiding hydromorphological degradation (Delgado et al., 2013; Osborne & Kovacic, 1993).

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

We conclude that research gaps regarding the impacts of diffuse urban stressors on stream ecosystems still exist. Some geographic areas (i.e., Global South) and target organisms (i.e., microorganisms) are still underrepresented in the scientific literature. We therefore highlight the need to address the impacts of urbanisation on stream ecosystems from the Global South. Our review also highlights that future studies on diffuse stressors of urban origin should address chemical stressors beyond inorganic nutrients, including common and potentially toxic urban pollutants such as heavy metals and xenobiotics, as well as their transformation products. Moreover, we stress the need to include microorganisms in future studies and mechanistically address how urbanisation alters the relationship between stream biodiversity and ecosystem functioning. These recommendations for future research directions will surely help improve our capacity to disentangle how urbanisation puts ecosystem functions and the ecosystem services relying on them at risk.

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CRediT Agreement Statement

Miriam Colls and Ferran Romero: Conceptualization, Data Curation, Formal Analysis, Fundraising, Research, Methodology, Project Management, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review and editing. All the other authors: Data Curation, Formal Analysis, Writing – Review and Edit.

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