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An overview of non-native species invasions in urban river corridors

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Abstract

Recent studies have highlighted cities as prime locations for the introduction, establishment and spread of non-native and invasive species. As the hydrological arteries of cities, urban river corridors have an important role to play in influencing species invasions. This overview examines existing literature to consider (1) how the landscape functions of urban river corridors (habitat, conduit, barrier/filter, sink and source) relate to species invasions; (2) the organismal and geographical foci of research into non-native species invasions along urban rivers; and (3) the need to more fully consider the roles that non-native species may play in the recombinant communities of novel urban river ecosystems. The review ends with an identification of research priorities at the intersection of urban river corridor function and invasion biology.

Keywords: Non-native, alien, invasive, urban, stream, river, corridor function

Word count: 6768 inc. references.

Introduction

Cities are centres for non-native species introductions, as well as sources for the spread of non-natives throughout surrounding regions (Aikio *et al.* 2012; Duquette *et al.* 2016; Padayachee *et al.* 2017). Their role as nodes in global trade networks facilitates the intentional and accidental introduction of species as people and goods circulate between cities, and their large human populations inevitably result in (for example) high numbers of non-native species planted in public and private green space (Padayachee *et al.* 2017). These trends are well known: Mack (2003) estimated between 7000-10000 species in transit globally via shipping on any given day, mainly to

urban ports, while multiple studies have observed notable proportions of non-native species in urban ecosystems (e.g. Tait *et al.* 2005; Kowarik *et al.* 2013).

Urban ecosystems have been the concern of only a relatively small portion of the biological invasion literature (Gaertner *et al.* 2017). Most studies that *are* concerned with urban non-natives have focused on terrestrial ecosystems, with aquatic urban ecosystems such as rivers, lakes and ponds being only a minority of cases: as of 4 March 2019, of 4,804 studies listed in Web of Science including the terms “urban*” AND the term “non-native*” OR “alien*” OR “invasive*” OR “exotic*”, only 90 (1.9%) focused on urban rivers, streams, lakes and ponds. Of these, 66 studies focused on urban rivers/streams. Likewise, these articles form only a small proportion (2.6%) of the 2,532 studies found using the search term “urban river*” OR “urban stream*”, indicating that invasion biology is only a relatively small focus within urban river research. These searches will not have encapsulated all studies into urban rivers and non-native species, but as a subset are indicative of the relatively limited extent of work performed to date. Nonetheless, there is growing interest in understanding patterns and processes of invasion in urban rivers, in part to prevent spread of non-natives within and without the city.

Freshwater invasions are inherently spatial, and are best explored at the landscape scale; rivers function as dynamic corridors conducting materials (including organisms) through the landscape, and a body of work has developed on riverine landscape ecology (or sometimes ‘riverscapes’) in recent decades (Haslam, 2008). This paper examines the existing literature on urban rivers and streams (hereafter ‘rivers’ as there is little technical distinction) to explore (1) interactions between urban river corridor functions (habitat, conduit, barrier/filter, sink and source) and non-native species invasions; (2) the geographical and organismal foci of research into non-native species in urban rivers; and (3) the role that non-native species play in novel urban river ecosystems and their recombinant communities. The term ‘river’ used here includes all riverine structural components, including riparian zones. The review ends with an identification of research priorities at the intersection of urban rivers and invasion biology.

The term ‘non-native’ is used here as a catch-all meaning any species introduced outside its natural range, and essentially synonymous with ‘alien’ and ‘exotic’. We do not distinguish between ‘non-native’ and ‘invasive’, recognising that whilst many species may be classified as ‘non-native’, only a small proportion will go on to be ‘invasive’, i.e. having detrimental ecological, societal or economic impacts (Caley *et al.* 2008).

Urban rivers as landscape corridors for non-natives

Urban rivers are typically ecologically degraded and have limited functionality compared to their more natural exurban counterparts (Petts *et al.*, 2002; Walsh *et al.* 2005). This trend has been encapsulated with the ‘urban stream syndrome’ (Walsh *et al.* 2005), which has highlighted a suite of common impacts of urbanisation within river catchments across hydrology, ecology, geomorphology and society, with growing evidential support (Table 1; cf Booth *et al.* 2016). These changes to riverine and riparian structure and processes are in many cases unprecedented, and have essentially created environmental conditions with limited, or no, natural analogues; to the extent that some have argued that urban rivers represent novel ecosystems (Catford *et al.* 2013; Francis, 2014). The ecological outcomes of such impacts often include a reduction in native species populations and diversity, and an increase in non-natives (Kuglerová *et al.* 2019).

Despite their often degraded state, urban rivers still fulfil landscape corridor functions; and each of these functions is important in the context of species invasions. Functions include (1) habitat, (2) conduit, (3) barrier or filter, (4) sink and (5) source (*sensu* Forman, 1996). These functions vary with river size and catchment position, reflecting variation in channel size and slope, discharge, sediment dynamics and so on (e.g. Poole, 2002), and the level of modification found in urbanised catchments creates complicated and heterogeneous responses throughout river networks (Gurnell *et al.* 2007), though there has so far been limited investigation across catchment or landscape scales.

The evidence for how these different corridor functions interact with non-native species, based on available literature, is now explored.

Habitat

Urban rivers exhibit degraded within-channel and riparian habitat (Kuglerová *et al.* 2019). Physical habitat is often simplified and homogenized, whether through removal or reconstruction of vegetation and bank habitat (e.g. hard engineering) or the interruption of natural processes (e.g. sediment transport and deposition). Such changes create challenges for ecological communities that are attuned to the original (pre-modification) habitat conditions, and can favour non-native species that are more able to exploit novel conditions (e.g. Nelson, 2011). Non-natives may (for example) be better able to tolerate stress or disturbance, may benefit from a lack of predators/herbivores,

and/or may be able to compete more effectively for resources. Certainly one of the most reported observations from urban rivers is that they tend to have notable proportions of non-native species, and that this is often higher than in exurban reaches (Engman and Ramirez, 2012; Landis and Leopold, 2014); though this is not a universal trend (Beauchamp *et al.* 2015). Proportions of non-native species vary according to location and community type (Table 2). These studies are broadly in line with urban ecosystems in general, which, while also variable, tend to have mean proportions of non-natives at around 10-35% (Francis and Chadwick, 2013).

Proportions of urban non-natives tend to increase over time (e.g. Kowarik *et al.* 2013). Few studies have looked at temporal change in non-native species along urban rivers, though Jackson and Grey (2013) noted that of the 96 non-native species recorded in the River Thames (UK) catchment, 53% (51 species) have established in the last 50 years; and that new invasions are recorded every 50 weeks on average. Leuven *et al.* (2009) explored the heavily modified and partly urbanised River Rhine catchment (Germany), and found an increase in invasion rate from <1 species per decade to 13, since the eighteenth century. Freshwater systems are amongst the most invaded globally (Francis and Chadwick, 2012), and urban riverine and riparian habitats are likely to be consistent hotspots of introduction and establishment, especially under conditions of growing urban populations and climate change (Catford *et al.* 2013).

Several studies have demonstrated the links between urban conditions and species invasion along rivers. There are broad-scale linkages between key urban indicators such as levels of impervious surface cover adjacent to rivers, and human population density, to the presence or abundance of non-natives (e.g. Dallimer *et al.* 2012; Kuglerová *et al.* 2019). Some studies have found more specific associations between urban river habitat conditions and the presence or abundance of non-natives, including changes in pH (Grella *et al.*, 2018), cultural eutrophication (King and Buckney, 2000), and disturbance regimes (MacCoy and Blew, 2005). Establishing drivers for species invasions in any habitat can be problematic (MacDougall and Turkington, 2005), and the complexity (and novelty) of environmental changes in urban river systems makes this especially challenging; but certainly changes in habitat conditions, combined with an abundance of source populations in association with human habitation and infrastructure, facilitates non-native introduction and establishment.

Species invasions can also change habitat conditions. In freshwater systems impacts of invasion include changes to biodiversity and community composition, physical habitat, ecosystem function

and resilience, and degradation of ecosystem services (Francis and Chadwick, 2012). In urban rivers, documented impacts include:

(1) Changes to the physical environment, particularly when species act as ecosystem engineers. Crayfish, for example, can have complex but profound negative impacts on submerged macrophytes, phytoplankton, nutrient dynamics and benthic macroinvertebrates by increasing sediment suspension and bioturbidity through feeding and burrowing activities (Matsuzaki *et al.* 2009), changing predator-prey relationships (Ficetola *et al.* 2012), and causing bank erosion (Faller *et al.* 2016). Non-native plants such as Japanese knotweed (*Fallopia japonica*) can cause high rates of bank erosion, particularly where channels are incised (Arnold and Toran, 2018), while non-native tree colonisation of bed sediments in reduced flows can lead to channel narrowing (MacCoy and Blew, 2005).

(2) Biogeochemical impacts, in particular changes in leaf litter and organic detritus resulting from invasion by non-native tree species, and the impacts this may have on macroinvertebrate or microbial communities that rely on such resources. Some studies have found little impact (Kennedy and El-Sabaawi, 2018), while others have determined lower macroinvertebrate abundance (Fargen *et al.* 2015), altered macroinvertebrate feeding groups or communities (Fargen *et al.* 2015), lower detritivore densities (Miller and Boulton, 2005) and increased occurrence of detritivores in association with non-native litter (Swan *et al.* 2008); or differences in decay rates (Swan *et al.* 2008).

(3) Changes in biotic interactions, such as competition (Masters and Emery, 2016) and predator-prey relationships that can lead to shifts in trophic position, as observed for fish (Lisi *et al.*, 2018) and reptiles (Wilhelm and Plummer, 2012) as diet becomes more focused on non-native consumption. Such changes are likely to be prolific, but remain largely unexplored.

Responses of other elements of urban river habitat structure and function to non-native invasion remain largely unexplored, for example how invasions may impact on habitat heterogeneity, seral processes, metapopulation dynamics and reproductive success. Such impacts are likely to be spatially and temporally complex, and the degraded nature of urban rivers makes isolating invasions as driving factors challenging. It should also be remembered that habitat changes are not always negative (Albertson and Daniels, 2016).

Conduit

Urban rivers conduct flows of water, sediment, nutrients, pollutants and biota through the urban landscape. Urban rivers are often regulated, with controls placed on their flow dynamics, meaning that the conduit function is suppressed compared to more natural rivers (Table 1; Kuglerová *et al.* 2019); though flashy responses to urban hydrological conditions can lead to pulses of material through the urban system. Flow connectivity within the catchment network is often restricted due to the presence of impoundments or other obstacles (discussed as barriers/filters below).

From patterns of plant and animal spread and propagule deposition observed, it seems that flows are often sufficient to enable the spread of non-natives through urban river catchments (e.g. Leuvan *et al.* 2009; Dallimer *et al.* 2012) and beyond (e.g. Foxcroft *et al.* 2007), though this will vary according to local conditions and organism type. Although base flows are often reduced in urban systems, peak and overbank flows can be increased, especially where urban river planning or management is ineffective or channels are no longer able to cope with changes to urban hydrology (Table 1). This leads to the deposition of species in riparian or bankside zones, and can also result in non-natives reaching other aquatic ecosystems (both natural and artificial), including drainage ditches, ponds and artificial wetlands.

Certainly direction and dimensionality of flows are important in influencing non-native spread, particularly for organisms reliant on flows for dispersal, such as hydrochorous plants. Dallimer *et al.* (2012) found that neophyte richness along rivers in Sheffield increased downstream – in most cases this resulted in increases in non-native plants in the urban core, but for a single river flowing out of the urban core the opposite trend was found, highlighting that flow direction (rather than simple urban proximity) was the key driver of spread.

Dispersal along urban catchments can be rapid. Leuvan *et al.* (2009) estimate rates of spread for several non-native macroinvertebrates within the River Rhine catchment to be 44-112km year⁻¹, with rates higher in larger reaches. Non-native plant propagules can be transported long distances. Säumel and Kowarik (2010) tested secondary dispersal of three non-native tree species along an urban river using tagged samaras. Although the number of propagules declined exponentially with distance from point of release, partly due to the influence of river traffic, a substantial proportion (20-25%) floated 1200m within three hours, with no interspecific differences; as 1200m was the limit of the experiment, it is likely that some samaras would have continued to float over greater distances.

As a result, the conduit function is very important for spread of non-native species through urban river catchments and their surrounding landscapes (Leuvan *et al.* 2009; Dallimer *et al.* 2012), though how this varies for different conditions and species within an urban context remains to be fully explored.

Barrier/Filter

Just as integral flows can be important, barriers to flow and organism movement will shape processes of non-native spread and establishment. Barrier and filter effects result from physical or environmental interruptions to system connectivity, for example resulting from impoundments, weirs or areas of shallow flow. Absolute barriers are rare, and most interruptions to riverine and riparian connectivity will have filter effects, restricting some species or individuals but not others (Catford *et al.* 2011). Loss of connectivity can impact native species, compromising their meta-populations and thereby encouraging community dominance by non-natives; as observed for some urban rivers on tropical islands (Ramirez *et al.* 2012). However, lack of connectivity can also help prevent non-native spread.

Filter effects may operate longitudinally and laterally. Longitudinal barriers may occur naturally, as change in habitat conditions (e.g. channel width, flow velocity, sediment coarseness, vegetation) with catchment position limit available habitat for non-native species (Kornis and Vander Zanden, 2010). For example, saltwater barriers between estuary catchments have been suggested to act as limits on the spread of non-native fish (Leidy *et al.* 2011); while a dry reach within the Santa Clara River in California (USA), containing water only in exceptional storm events, was found to limit 'genetic dilution' of a native population of the Santa Ana sucker (*Catostomus santaanae*) by a non-native sucker present downstream (Richmond *et al.* 2018).

Anthropogenic barriers can also be effective in preventing the spread of non-natives through river systems, including urbanised catchments; for example, Bentley (2012) notes that the upstream migration of Chinese mitten crabs (*Eriocheir sinensis*) may be blocked by weirs. Multiple barriers can be especially effective in restricting movement (Favaro and Moore, 2015), and intentional fragmentation has been suggested as a prevention strategy for aquatic invasions (Rahel, 2013).

The capacity of urban rivers to act as lateral filters for organism movement in the urban landscape is poorly understood. River channels in general can act as behavioural filters for the movement of organisms, with for example forest bird communities being different on either side of large rivers (Heyes and Sewlal, 2004). Tremblay and St. Clair (2009) found that urban rivers were more effective barriers to bird movement than roads, railways and bridges, possibly because of an intuitive aversion to rivers as areas of high predation risk or territorial boundaries, but also because of a lack of vegetation, which was found to be important for movement across barriers in general. Lateral filter effects are generally unknown, though many urban organisms tend to be generalists that can move over barriers more easily, and so filter functions may also be suppressed in the urban environment, as species negatively impacted may already have been lost from the urban landscape.

Sink

Rivers occupy areas of low elevation, and are therefore repositories for sediments, nutrients, propagules and pollutants. This is particularly the case in urban catchments, where high levels of impervious surface cover results in substantial increases in runoff following rainfall events, which, in combination with storm drains and sewerage networks (e.g. combined sewer overflow outfalls), can wash seeds and other materials into urban rivers. Zedler and Kercher (2004) note that wetlands dominated by surface runoff are especially vulnerable to invasion, and this is likely another driver of high proportions of non-natives in urban rivers.

Certainly urban rivers may accumulate and transport (see above) huge numbers of propagules. Hoggart and Francis (2014) placed 180 coir rolls (total volume around 4000 m²) along walls of the River Thames to sample the mobile seed bank. Following translocation to a laboratory environment, over 7,600 seeds germinated from the rolls, of which 11% were from a single non-native species: *Buddleja davidii*. The sink function is also reflected in riparian soil seed bank studies, where germination experiments have found abundant seeds, with significant proportions of non-natives (e.g. 21% of germinated seeds along the River Brent, UK; Cockel and Gurnell 2012). Landis and Leopold (2014) surveyed the riparian seedbank of an urbanised stream in Syracuse, NY, and found that non-native species accounted for around 25% of all germinants.

Presence in the seed bank is also reflected in riverine and riparian community composition; for example, Stromberg *et al.* (2016) observed that many urban riparian species in the Salt River (USA) were trees cultivated in nearby cities, while Meek *et al.* (2010) found that riparian non-native plant

cover was highest in areas bordered by urban land. In this way, urban areas directly contribute non-native species to rivers from their component ecosystems (gardens, parks, brownfield sites etc.).

While there has been substantial focus of research into urban rivers as sinks for pollutants (Scholes *et al.* 2008) and more recently plastics (Nel *et al.* 2018), more work is needed on patterns and processes of non-native species accumulation, and river and riparian seed banks in particular.

Source

Urban rivers both accumulate and disseminate non-native species from and through the surrounding landscape, and therefore are a source for invasions. Urban areas are suggested to be sources of non-native species invasions outside urban regions, with, for example, Aikio *et al.* (2012) finding that first records of non-native species are associated with proximity to urban areas; and also that ‘urban’ and ‘streamside’ habitats were frequent sites of initial invasion. This suggests that urban rivers may act as both initial sources of non-native spread, and reservoirs of propagules that may disseminate along river networks if conduit functions allow – though direct observation and quantification of this is rare. For example, Duquette *et al.* (2016) observed that riparian Japanese knotweed (*F. japonica*) distributions were associated to proximity with nearby towns and villages.

The source function is arguably one of the most important in terms of facilitating invasions through the landscape (aquatic, riparian and terrestrial), but has received little attention in an urban context. The active role of urban rivers in facilitating spread to exurban regions remains to be more thoroughly investigated.

Geographical spread and organism focus of urban river invasions research

To obtain a broad picture of the geographical spread and organism focus of urban river invasions research, a Web of Science search using the terms “urban*” AND the term “non-native*” OR “alien*” OR “invasive*” OR “exotic*” was executed (n = 4,804), then narrowed to incorporate only those studies focused on “urban river*” OR “urban stream*” (n = 65). These search terms were used to narrow the focus to those studies that focused specifically on urban river/stream and invasion research, as the incorporation of broader terms (e.g. “city”, “channel”, “river”, “stream” or “riparian” more generally) found many studies that included these terms incidentally (e.g. in location or place names) or only very peripherally or tangentially related to urban river, stream or riparian-

specific invasions. This body of work was then supplemented with further literature searches using Google and Google Scholar (including grey literature), to result in 77 studies with a focus or part-focus on non-native invasions in urban rivers/streams. These were then classified according to organism focus and study location (where applicable). Some studies examined more than one organism type, and so were counted twice.

The majority of studies (56%) focused on plant species, with macroinvertebrates (32%) and fish (18%) following. A smaller number of studies focused on avifauna (4%), bacteria (4%), annelids (4%), fungi (3%), amphibians (3%), mammals (3%) and reptiles (1%). Most studies (84%) focused on a single organism type. This distribution of organism foci generally reflects that observed in non-native/invasive species records globally (Turbelin *et al.* 2017). Plants account for the majority of records in invasion biology and create a significant bias in research (Turbelin *et al.* 2017). Insects and fish are also relatively abundant in records and urban river studies in general (Wenger *et al.* 2009), and this trend is echoed here. Macroinvertebrates in particular are a staple of freshwater ecology research and their presence in so many studies here is unsurprising. The relative lack of studies into mammals and avifauna, in contrast with global invasion records (Turbelin *et al.* 2017), probably reflects the general paucity of such taxa in urban rivers (Wenger *et al.* 2009).

The geographical distribution of work to date also largely reflects that of species invasion records, with North America (mainly the USA) being the location of most work (44%), followed by Europe (29%) and Australia/New Zealand (13%). South America (9%), Africa (3%) and Asia (3%) are in the minority. This pattern also indicates not only research capacity and English language bias, but also history of urbanisation and river modification, as those regions that urbanised earlier, and thus have longer-standing documented invasions and urban river impacts, have seen the most research. This does highlight the need for greater research in developing and rapidly urbanising countries such as Asia and Africa, which are also likely to see rapid increases in species invasions.

This is a relatively small body of literature that may not be fully comprehensive, but it is indicative that urban river invasions research follows broader patterns observed across other ecosystems. There is a need for studies that incorporate multiple taxa, that consider geographical regions not well represented, especially those undergoing rapid urbanisation where before/after effects could be measured, and that have a more comparative approach.

The good, the bad and the uncharismatic

Biological invasions are recognised as threats to ecosystems globally. Urban rivers are no exception, in that exposure to non-native species can lead to ecological, socio-economic and cultural impacts, despite their already degraded state. It is nonetheless important to recognise that not all non-native species are problematic; only a small proportion become invasive (Caley *et al.* 2008), and some non-natives contribute useful functions to the communities they establish within, or to ecosystem services more broadly (Schlaepfer *et al.*, 2011; Trueman and Erber, 2013). There has been little research into non-impactful assimilation of non-natives into ecological communities, or positive benefits, with most work focusing on individual species, and particularly those with observed negative impacts. Often, the simple designation of species as non-native (or alien, exotic, non-indigenous or invasive) labels them as problematic and makes them uncharismatic and unappealing, regardless of their functional role within an ecological community.

Interestingly, this perception is most often challenged in urban ecosystems, because of the recognition that non-natives will continue to be part of urban ecological communities, and because urban communities do not hold to traditional community typologies (Rotherham, 2017). Indeed, study of cosmopolitan, recombinant communities – those formed of species that originate from a range of habitats, and which often include non-native species – has often taken place in urban ecosystems, including urban rivers (Francis and Hoggart, 2012; Rotherham, 2017). Urban river conditions can create locally unique communities, especially around novel habitats, as observed by Nelson (2011) for macroinvertebrates and McLellan *et al.* (2010) for microbes in sewerage systems. Such assemblages also lead to increased chance of species hybridization, as well as greater rates of phenotypic change (Alberti *et al.* 2017).

Non-native species and their recombinant characteristics have also influenced urban river restoration efforts and frameworks (e.g. Richardson *et al.*, 2007; Meek *et al.* 2013). The removal of non-natives is often one objective of restoration or rehabilitation techniques, though so far studies have indicated only limited success, with non-natives recolonising restored channels rapidly after interventions (e.g. Suren, 2009; Arango *et al.* 2015). Even extensive restoration can show limited reduction of non-natives, leading to several authors to recognise that non-natives and the recombinant communities of which they are a part are relatively unavoidable, and that urban rivers should be more adaptively managed as novel ecosystems to maximise ecological community function rather than native composition (Meek *et al.*, 2010; Francis, 2014).

Urban rivers are microcosms of urban ecological processes and how these may affect community structure and function, including non-native spread, establishment and impact. They represent important field sites for such investigations, and are an opportunity for urban ecology and invasion biology that deserves greater research focus.

Research priorities at the intersection of urban river corridor function and species invasions

Urban rivers occupy only a small part of the literature on riverine landscapes and non-native species invasions, and as such, corridor functions are poorly understood. There is a need for greater fundamental research on how corridor functions influence introduction, establishment, spread and impact of non-natives in urban systems; and likewise how invasions influence function. In the urban context, more research is especially needed on:

- Comparison of pre- and post-urban river function in relation to patterns and processes of invasion. Before-After-Control-Impact research designs in urbanising areas will help to more accurately determine drivers of change and response; this should include rigorous quantification of pre- and post-urbanisation conditions, rather than just comparison of urban with non-urban reference reaches, to more accurately pinpoint changes resulting from urbanisation. The greatest opportunities for such comparative research are in rapidly urbanising countries in Asia and Africa; regions that are somewhat under-represented (with the exception of China) in both urban river and invasion biology research (Francis, 2012; Turbelin *et al.* 2017).
- Systemic spatio-temporal changes in river function and invasion response through urban river catchments. This should be placed within the wider riparian/landscape context and should take into account both systemic changes that would occur naturally within the catchment (e.g. functional and community changes associated with the river continuum) as well as anthropogenic drivers, such as those associated with varying urban stream syndrome characteristics (Table 1).
- Comparisons of inter-relationships between function and invasion across multiple (rather than single) taxa, and across a broader range of organisms, especially broadening investigations beyond plants, fish and macroinvertebrates.
- Comparison of urban river systems geographically, to avoid reliance on unique case studies and address geographical variation in response. Despite commonalities in urban stream syndrome characteristics, each river catchment, and indeed individual reaches, have specific

and unique characteristics that will influence patterns and processes of invasion (e.g. Brierley and Fryirs, 2009); as will the biogeographic context the catchment is situated within (Richardson *et al.* 2007). This includes the wider environmental and ecological urban context of the river, which will present its own characteristics and idiosyncrasies. While this should not stop generalisations and broad trends from being elucidated, the high level of geographical variability should be appropriately investigated.

- Exploration of urban rivers from more varied climatic, developmental and biogeographical regions (not just temperate cities in developed countries) to more fundamentally understand how patterns and processes of invasion vary.
- Consideration of the role of non-natives in recombinant communities, and their negative, neutral and positive impacts. This will in particular involve research into the capacity of such species to provide ecosystem services (and disservices), and will utilise knowledge and methods from (among other areas) river restoration, ecological economics, citizen science, and environmental psychology to appropriately engage various stakeholders in urban rivers and their communities.
- How urban river corridor functions and invasions may be influenced by broader global and regional environmental changes (e.g. climate change, pollution, biodiversity loss).

Data availability statement: Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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Domain	Feature	Potential Symptom*	Urban-specific drivers	Influence on invasions
Physical	Hydrology	More overland flows; Faster rise to peak flows; Higher storm discharge; Decrease baseflows; Increased baseflows; Increased frequency of overbank floods	Changes in storm hydrology relate to decreased infiltration and increased runoff related to increased impervious surfaces; changes in baseflow relate to increased water abstractions and decreased groundwater recharge affecting groundwater levels; bed downcutting can increase surface water via reduced hyporheic habitat volumes; point sources can raise average discharges.	Changes in disturbance regimes can remove or reduce native communities and support dispersal and establishment of non-natives; overland flows transport non-native propagules from urban land cover to the river.
	Temperature	Increased stream water temperature	Urban heat island; hotter than ambient discharges.	Warmer temperatures can favour non-natives from warmer climates.
	Geomorphology	Increased channel width; Scouring; Accumulation of fine sediments; Increased substrate embeddedness; Modified sediment loads	Modification to hydrology (see above) and sediment supply from catchment-level urban development; channelization, habitat simplification and modification for flood control affects scouring flows and sediment supply at reach-scales.	Changes in disturbance regimes as noted above for hydrology; newly scoured or deposited sediment can be rapidly colonised by non-natives.
	Instream habitat	Decreased habitat complexity; Changes in habitat dimensions (e.g. pool depth); Culvert, weirs, modified channels	Modified hydrology, geomorphology and addition of anthropogenic structures (e.g., weirs, culverts, banks modifications) lead to simplification and destabilized dynamics.	Simpler habitats (and particularly artificial structures) may be more susceptible to invasion.
	Riparian habitat	Loss of bankside vegetation; Increased light	Loss of species richness due to land clearing and flood management activities; increases in lawns and parks with decreases in trees; flooding scours riparian habitats	Degraded native communities offer opportunities for non-native colonisation, especially when planted in riparian or adjacent zones.
Chemical	Point Sources: Sewage Industrial Waste	Increased nutrients; Increase organic matter loading; Industry related pollutants	Wastewater and industrial effluents; combined sewer overflows.	Eutrophication may further favour non-natives that already have a competitive advantage over natives, or that have a higher tolerance for pollution.
	Non-Point Sources: Macronutrients	Increased nutrients; Sediment loading;	Non-point source runoff of terrestrial derived pollutants;	

Toxics		Pesticides; Contaminated road runoff;		
Biological	Algae	Decreases in richness and abundance of sensitive taxa with corresponding increases in tolerant taxa;	Impaired water quality and loss of habitat decreases overall biodiversity;	Degraded and simplified native communities create niches and offer opportunities for non-native colonisation and dominance; non-natives can facilitate further non-native invasions of associated species.
	Invertebrates		Changes in habitat structure affects animal behaviours;	
	Fish	Simplification of food webs via loss of sensitive taxa;	Acute mortality event and chronic toxicity from degrade water quality.	
	Riparian vegetation	Potential increases in invasive and non-native species;		
	Water bird	Modified links between aquatic and terrestrial species		
Ecological	Riparian animals			
Ecological	Ecosystems	More work needed to elucidate how both ecosystem functions and services are modified by urbanization of aquatic systems; degradation of urban systems are linked to over-extraction of ecosystem services (e.g. waste assimilation associated with sewage effluents)	Modification of natural process at catchment scale (i.e. land use changes with increased impervious surfaces) and finer scales (e.g. habitat modifications; local pollution).	Disturbances, interruptions and modifications to functions and services offer opportunities and facilitate invasions as noted above for individual features.
	Functions			
	Ecosystems Services			

688 Table 1. Summary of the Urban Steam Syndrome with evaluation of physical, chemical, biological and ecological patterns, and indications of how patterns
689 can influence species invasions (modified from Walsh *et al.* 2005, Richardson *et al.* 2007; Wenger *et al.* 2009, Kominkova 2012, Hale *et al.* 2016).

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Location	Organism type	Finding	Source
Riparian zones of urban rivers in Sheffield (UK)	Plants	28% of plant species were neophytes, (introduced after 1500 AD) with a further 8% archaeophytes (introduced before 1500 AD)	Dallimer <i>et al.</i> (2012)
Riparian zones of urban rivers in Sheffield (UK)	Birds	3 out of 74 (4%) bird species were non-native	Dallimer <i>et al.</i> (2012)
Urban streams in Manaus (Brazil)	Plants (woody)	15% of woody species were non-native.	dos Anjos Santos <i>et al.</i> (2016)
Riparian zones of an urban stream in NY (USA)	Plants	51% non-native species (34% at more rural sites).	Landis and Leopold (2014)

Urbanised catchment in Puerto Rico (USA)	Fish	5 out of 11 (45%) species were non-native.	Engman and Ramírez (2012)
Urban streams of Toledo, Southern Brazil	Fish	4 out of 26 (15%) species were non-native.	Daga <i>et al.</i> (2012)
Urban river walls of the River Thames, London (UK)	Plants	14 out of 90 (16%) species were non-native.	Francis and Hoggart (2012)
Streams of the urbanized San Francisco Estuary, California	Fish	7 out of 17 (41%) species were non-native.	Leidy <i>et al.</i> 2011
Urban streams in the Santa Ana River basin, CA (USA)	Fish	12 of 16 species (75%) were non-native.	Brown <i>et al.</i> (2005)
Urban riparian zones in SW Poland	Plants	9% of plant species were non-native.	Stefanska-Krzaczek and Podgrudna (2015)
Urban riparian soils in the River Brent, London (UK)	Plants	21% of species observed from the seed bank were non-native.	Cockel and Gurnell (2012)
Mobile seed bank along the River Thames, London.	Plants	33% of species observed from the seed bank were non-native.	Hoggart and Francis (2014)
Urbanised River Rhine catchment in Germany	Macroinvertebrates	11.3% of species were non-native on average across different freshwater sections of the river.	Leuvan <i>et al.</i> (2009)

Table 2: A sample of studies showing proportions of non-natives in ecological communities.