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Piatã S. Marques, Luisa R. Manna, Rosana Mazzoni, & Rana El-Sabaawi

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Intraspecific trait variation in urban stream ecosystems: toward understanding the mechanisms shaping urban stream communities

Piatã S. Marques[1,3], **Luisa R. Manna**[2,4], **Rosana Mazzoni**[2,5], **and Rana El-Sabaawi**[1,6]

[1]Department of Biology, University of Victoria, Victoria, British Columbia, Canada V8P 5C2
[2]Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, 20550-900 Rio de Janeiro, Brazil

Abstract: The rapid expansion of urban centers is a critical threat to stream ecosystems, yet we currently lack mechanistic understanding of the effects of urbanization on stream communities. Here we explore how an intraspecific trait perspective can unveil mechanisms of change in urban stream communities. Intraspecific trait approaches are rarely used in urban aquatic ecosystems though their potential has been widely demonstrated in terrestrial systems. We begin by identifying several biotic and abiotic agents that can drive intraspecific trait changes in life history, behavior, morphology, and feeding in a range of urban stream organisms. We then propose that intraspecific trait-based approaches in urban streams can help explain the mechanisms underlying species persistence, biodiversity responses, functionality, and evolution and how they can potentially improve biomonitoring in urban streams. This trait-based information is essential to better understand, predict, and manage the impacts of urbanization on stream biota.

Key words: urban phenotype, plasticity, adaptation, evolution, trait interactions, anthropogenic impact, cities

Over the last few decades, ecosystems have been under an increasing number of threats associated with human activities, many of which are related to land use change and urbanization (Strayer and Dudgeon 2010). Currently, 54% of the world's population lives in cities, and this number is expected to reach 66% by 2050 (United Nations 2014). This trend suggests potential increases in the magnitude of urban impact to ecosystems worldwide in the near future. Urbanization affects natural ecosystems through habitat degradation, species loss, disruption of ecosystem processes, and biological interactions (Alberti 2008). In stream ecosystems, urban development leads to a collection of symptoms known as "the urban stream syndrome" (USS) that include severe environmental degradation, species loss, and dominance of a few tolerant taxa (Walsh et al. 2005).

Research on the effects of urbanization on ecosystems has produced a large volume of literature, but the mechanisms driving the effects of urbanization on biodiversity remain unclear (McDonnell and Hahs 2013). The majority of studies focus on the community-level numeric responses to urbanization, emphasizing the lethal effects on species (e.g., species loss) and changes to biodiversity (McDonnell and Hahs 2013, McDonnell and MacGregor-Fors 2016). However, species known as urban dwellers are able to persist and flourish despite urban disturbance (Fischer et al. 2015). How and why species thrive in urbanized ecosystems remains a fundamental yet unanswered question (Mouillot et al. 2013).

Changes in environmental conditions can cause plastic or genetic responses in life history, morphology, and behavior within and between populations (Mouillot et al. 2013). Humans can cause dramatic intraspecific trait changes through harvesting, pollution, climate change, species introduction, and landscape alteration (Darimont et al. 2009, 2015, Palkovacs et al. 2012). Intraspecific traits can be highly sensitive to environmental change because selective pressure operates on individuals, creating plastic and genetic responses

E-mail addresses: [3]piata@uvic.ca; [4]luisamanna@gmail.com; [5]mazzoni@uerj.br; [6]rana@uvic.ca

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in phenotype that can affect a range of ecological processes (Reznick et al. 2001, Matthews et al. 2010, Verberk et al. 2013). Therefore, characterizing intraspecific trait responses is an important component of understanding the impacts of anthropogenic change.

Recent work in terrestrial systems has shown that urbanization can be a major force driving intraspecific trait change (Alberti et al. 2017b). Temperature can drive the phenology of urban Brittlebush (*Encelia farinose*) populations (Neil et al. 2014), city noise causes Blackbirds (*Turdus merula*) to sing at higher frequencies (Nemeth et al. 2013), and increased predation risk in cities affects the wing morphology of the European Starling (*Sturnus vulgaris;* Bitton and Graham 2015). Such studies have been instrumental in revealing mechanisms by which terrestrial organisms respond to urban pressure because they can link specific urban impacts to phenotypic change (Alberti et al. 2017a). For instance, feeding plasticity has been hypothesized to be a key mechanism for the success of terrestrial urban species because it allows continued access to high-quality foods under altered food availability conditions (Shochat et al. 2010).

In contrast, much less is known about how urbanization affects intraspecific traits in aquatic ecosystems in general and in stream systems specifically. In this review, we propose that understanding how intraspecific traits vary in response to urbanization can help us tackle important mechanistic questions in urban stream ecosystems. We begin by identifying potential selective forces that can operate in urban streams. We use examples from urban and nonurban studies to highlight which traits can come under selection in the urban environment. We then identify important mechanistic questions about urban streams that can be addressed by characterizing intraspecific trait variability.

WHAT CAN CAUSE INTRASPECIFIC TRAIT CHANGE IN URBAN STREAMS?

The USS describes a collection of symptoms commonly observed in urban streams: reduced biotic richness, altered hydrography, elevated concentrations of inorganic dissolved N and P, and high contaminant concentrations (Walsh et al. 2005). Local environmental conditions and socioeconomic aspects of human communities can alter local symptoms (Booth et al. 2016, Parr et al. 2016), but the USS is nonetheless useful for describing the general state of urban streams. Here we use the USS as a starting point to facilitate the identification of agents of selection operating in urban streams. We use research from nonurban streams to explore how organismal traits might respond to these agents. However, in all of these nonurban stream examples we focus only on species that are known to occur in urban environments (Table S1). Finally, we use examples from urban systems, when they are available, to confirm whether trait responses that occur in nonurban systems also occur in urban systems. Our goal is to identify various pathways for intraspecific trait change to occur in streams altered by urban development. We highlight some of these pathways in Fig. 1.

Reduced biotic richness

Urbanization can affect species richness by removing sensitive species and promoting the establishment of tolerant or invasive species (McKinney 2002, 2008, Alberti 2008, Shochat et al. 2010). The combination of local extirpation and introduction/invasion determines community composition in urban ecosystems (Aronson et al. 2014). These changes in community composition can lead to intraspecific trait variability by disrupting ecological interactions (Bolker et al. 2003, Schmitz et al. 2004).

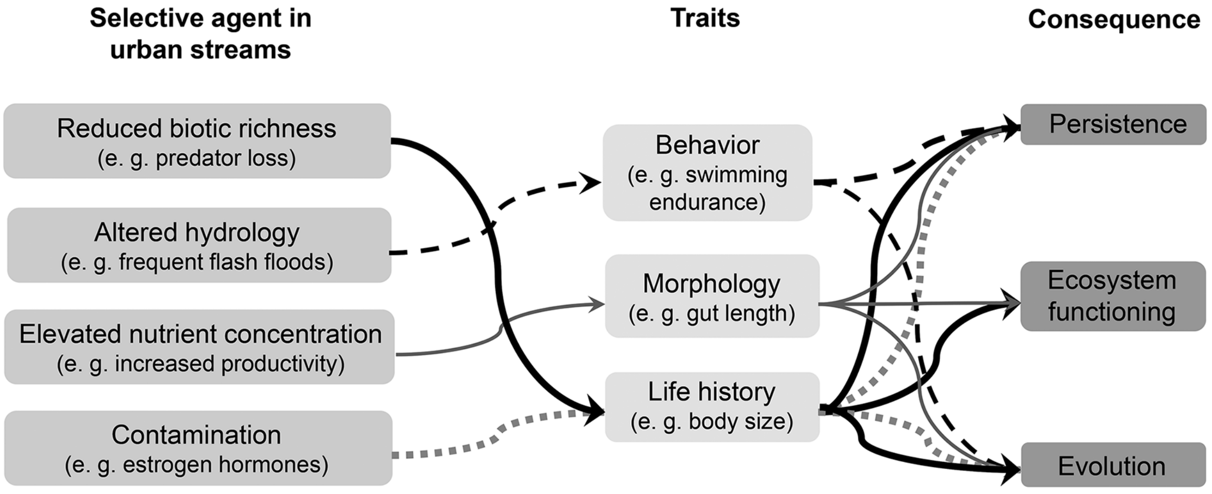

Figure 1. Examples of how an intraspecific trait perspective can help reveal and explain mechanistic change in urban streams. Examples are based on studies cited or mechanisms proposed in the text. Different arrows connect specific selective agents in urban streams to changes in intraspecific traits and the consequences of trait changes to ecological processes.

Extirpation is likely to disproportionately affect predator–prey interactions in urban streams because predators are especially vulnerable to environmental changes (Woodward 2009, Woodward et al. 2012). Studies in natural freshwater systems suggest that both predation release (i.e., absence of predator via extirpation) and predation risk (i.e., presence of predator via introduction) can drive changes in prey behavior, morphology, and life history with implications for prey survival (McCollum and Leimberger 1997, McCoy and Bolker 2008, Ahlgren et al. 2011, Hoverman et al. 2014). For example, predation risk decreases size at maturity while increasing reproductive allotment in the Guppy (*Poecilia reticulata*; Reznick and Endler 1982, Reznick et al. 2001). Predators can also affect the life-history traits of invertebrates and frogs (Laurila et al. 1997, Latta et al. 2007).

Invasion likely affects competitive interactions in urban systems. Invasive species can take advantage of altered urban environments to proliferate at large densities (Havel et al. 2015, Alberti et al. 2017a). High density of invasive species can increase intra- and interspecific competition (Shochat et al. 2010), which can alter intraspecific traits in both the introduced and the resident species. For example, in nonurban streams, invasive larval Bullfrogs (*Rana catesbeiana*) reduce the growth rate of native larval frogs (Kupferberg 1997).

Predation and competition can interact to drive trait changes in multiple species (Schmitz et al. 2004, Ohgushi et al. 2012). This interaction suggests that reported extirpation and species introductions in urban streams can also result in a cascading series of direct and indirect trait changes in multiple consumers. Although the effects of species removal or addition on intraspecific traits in urban streams have not been studied, urban stream food webs are typically highly altered (Warren et al. 2006, Yule et al. 2015), increasing the potential of intraspecific trait responses (solid black arrows in Fig. 1).

Altered hydrography

Urbanization alters stream hydrology mainly through its effects on stormwater runoff (Burns et al. 2015). The large amount of impervious surfaces in cities prevents stormwater from percolating into the soil. This increases the volume of stormwater that runs off to streams. Runoff water can alter base flow and increase the frequency and intensity of high flow events (Walsh et al. 2005, Luthy et al. 2015). This effect is exacerbated by the stormwater drainage system, which concentrates and directly discharges stormwater runoff into streams (Walsh et al. 2012). Urban stream hydrology can be further altered by channelization in which stream channels are often straightened, deepened, and lined with concrete (Paul and Meyer 2001).

Variation in hydrology has been shown to drive intraspecific trait change in many taxa in nonurban systems. High flow increases egg size in *Cyprinella venusta* (Machado et al. 2002). Changes in streamflow can also affect morphological traits in both snails and fish (Franssen et al. 2013, Gustafson et al. 2014). In urban streams, measuring how intraspecific traits respond to differences in the flow regime can help us understand how organisms cope with the variability in hydrology (Blanck and Lamouroux 2007, Mims and Olden 2013). For example, Nelson et al. (2015) have shown that flashier hydrology boosts the swimming performance of the Blacknose Dace (*Rhinichthys atratulus*) in urban settings. Shifts in swimming performance can be a mechanism that allows the biota to survive the extreme flows and flash floods in urban streams (dashed black arrows in Fig. 1).

Elevated nutrient concentrations

The urban environment is a major source of nutrients to streams. Roads, lawns, and landfills are sources of both dissolved inorganic N and inorganic P that are washed into urban streams by stormwater runoff (Carey et al. 2013). This effect is exacerbated by stormwater drainage systems that quickly deliver large volumes of stormwater runoff to streams (Bernhardt et al. 2008, Walsh et al. 2012). N and P found in stormwater can have various origins ranging from pet waste to household fertilizers (Carey et al. 2013). Wastewater can also be a major source of N and P to urban streams. The specific sources vary with economical development and the condition of the sewer system. In developing countries, the lack of sewer infrastructure causes untreated wastewater to be directly delivered to urban streams (Capps et al. 2016). The use of either combined sewers, leaky septic tanks and pipes, or both allows untreated wastewater to reach the stormwater system that drains into streams in some old cities (Bernhardt et al. 2008). Outflows from wastewater treatment plants often drain to streams and can also carry high loads of N and P (Carey and Migliaccio 2009).

The addition of N and P to urban streams increases nutrient concentrations, causing eutrophication (Conley et al. 2009). Inorganic N and P are important limiting nutrients governing both primary productivity and the availability and nutritional quality of basal food resources in freshwater systems (Stelzer and Lamberti 2001, Fields and Kociolek 2015). Food quantity (i.e., food abundance; Robinson and Parsons 2002) and food quality (i.e., food nutrient content; Jonsson et al. 2013) affect the traits of many aquatic taxa in nonurban systems. For example, changes in nutrient concentrations can affect the lipid content of diatoms (Fields and Kociolek 2015). Food availability affects fecundity and timing of sexual maturity in freshwater snails (Tamburi and Martín 2011). It also affects foraging behavior, habitat use, brood size, offspring size, interbrood interval, and morphology in Guppies (Reznick and Yang 1993, Robinson and Wilson 1995, Kolluru and Grether 2005). Increased food availability has recently been suggested to relax life-history trade-offs and affect sexual traits in many aquatic taxa, including *Daphnia* sp. and fish (Snell-Rood et al. 2015).

Food quality can affect growth and time of maturity in amphipods (Delong et al. 1993) and fish (Jonsson et al. 2013) and morphology in *Spea* tadpoles (Pfennig 1990) and cichlids (Muschick et al. 2011). For species that heavily depend on body coloration for mating (e.g., Guppies), the quality of food may also restrict the expression of color pigments, therefore affecting individual reproductive success (Grether and Kolluru 2011).

Studies from urban streams confirm that altered food availability and quality can produce intraspecific changes in feeding strategy, morphology, and life history. For example, Tófoli et al. (2013) have suggested that altered prey diversity induces a generalist feeding strategy on the urban catfish *Imparfinis mirini*. Mutchler et al. (2014) have proposed that altered food availability in urban streams changes gut morphology of the Stoneroller (*Campostoma oligolepis*). Filgueira et al. (2016) suggest that increased food availability changes body size of the Central Mudminnow (*Umbra limi*). Therefore, intraspecific changes in trophic traits are likely ubiquitous in urban streams and are likely important for explaining patterns of persistence and extirpation (solid gray arrows in Fig. 1).

Contaminants

Cities are major sources of water contaminants, defined here as chemicals that can cause sublethal effects on aquatic organisms. Contaminants such as heavy metals, pesticides, and road salt are washed from lawns and roads by stormwater runoff and delivered to urban streams mainly through the stormwater drainage system (Kim et al. 2005, Weston et al. 2009, Gardner and Royer 2010, Zgheib et al. 2012). Contaminants such as pharmaceuticals are found in wastewater, which is directly discharged into urban streams when sewage systems are unavailable (Thomas et al. 2014). Such contaminants can also reach streams in cities where faulty or combined sewers allow wastewater to enter the stormwater drainage system (Panasiuk et al. 2015). Outflows from wastewater treatment plants often drain into urban streams and can also carry high concentrations of pharmaceuticals (Batt et al. 2006).

Contaminants such as heavy metals, pesticides, and road salt are known to lead to intraspecific trait changes in nonurban stream biota. For example, cadmium and copper impair growth and reproduction in *Daphnia magna* (Knops et al. 2001). The Poeciliid fish *Gambusia affinis* has lower reproductive investment and smaller male size in sites affected by lead–zinc mining effluent (Franssen 2009). Laboratory experiments suggest that pesticides reduce the growth of the midge larvae *Chironomus javanus* (Somparn et al. 2017). High salt concentrations can potentially indirectly affect intraspecific traits by altering biotic richness (e.g., excluding salt-intolerant species, such as salamanders [*Ambystoma maculatum*] or frogs [*Rana sylvatica*]; Collins and Russell 2009).

Pharmaceuticals such as sterols, caffeine, antidepressants, antibiotics, environmental estrogens, and in some cases cocaine compounds have all been reported in urban streams (Kolpin et al. 2002, 2004, Thomas et al. 2014). This problem is exacerbated by increases in flow variability (Kolpin et al. 2004). Evidence from nonurban streams suggests that these chemicals can cause trait changes. Norfluoxetine, a residue from antidepressant (Prozac®), induces spawning in *Dreissena polymorpha* bivalves (Fong and Molnar 2008), while plant sterols can lead to masculinization of female Poeciliid fish (Bortone and Davis 1994). In urban streams, estrogens from wastewater effluents cause intersexualization of White Suckers (*Catostomus commersoni*) and demasculinization in Fathead Minnows (*Pimephales promelas*; Woodling et al. 2006, Vajda et al. 2011). Changes in traits related to reproduction are likely to disrupt population dynamics and affect species persistence in urban streams (Hutchings et al. 2012; dotted gray arrows in Fig. 1).

Interacting agents of trait change in urban streams

We have thus far outlined how individual stressors can influence the intraspecific traits of stream biota. It is important to note that stressors can interact and be confounded (Craig et al. 2017). For example, urban stormwater runoff and the associated stormwater drainage network is an important source of stress to urban streams (Walsh et al. 2012). Stormwater input not only changes hydrology but can also contribute to thermal stress, change turbidity, and increased nutrient and contaminant concentrations. Each of these additional stressors is known to produce changes in traits such as life-history patterns (Robinson et al. 1992, Seehausen et al. 1997, Mladenka and Minshall 2001, Engström-Öst and Candolin 2007, Somparn et al. 2017). Also, to cope with added water volume, the morphology of urban stream channels is often altered. Channel modification affects hydrology and reduces species richness through simplification and homogenization of habitats (Paul and Meyer 2001, Walsh et al. 2005). Both changes in hydrology and species loss can lead to changes in species morphological traits (Pfennig and Murphy 2002, Franssen et al. 2013, Gustafson et al. 2014). In addition, riparian deforestation occurs in association with urbanization (Paul and Meyer 2001, Walsh et al. 2005). Loss of riparian vegetation increases in-stream temperature and light incidence, which can affect algal traits (Butterwick et al. 2005). Interacting stressors can have synergistic, antagonistic, and additive effects on traits (Coors and De Meester 2008). However, such effects have not yet been assessed in urban stream organisms.

APPLICATION OF TRAIT-BASED APPROACHES TO URBAN STREAMS

By viewing the components of the USS as drivers of trait change, we have demonstrated that there is a large potential for intraspecific trait changes to occur in urban streams (Fig. 1). It is therefore likely that an "urban phenotype" emerges as a response to urbanization across a wide range of aquatic taxa (Alberti 2015). These trait changes can be either plastic or heritable and have either ecological or evolutionary consequences. Yet, to our knowledge, there are few studies on how intraspecific traits of stream organisms change in response to urbanization, which we have highlighted in the previous section (Woodling et al. 2006, Chaves et al. 2011, Tófoli et al. 2013, Mutchler et al. 2014, Murphy et al. 2015, Nelson et al. 2015, Filgueira et al. 2016). While these studies describe intraspecific trait changes that appear to be caused by some of the urban stream selective agents described here, many questions remain regarding the mechanisms responsible for these shifts. Answering these questions can benefit from an intraspecific trait perspective in urban streams.

Why do some species persist in urban ecosystems?

Urbanization is an important driver of global species decline (Aronson et al. 2014). Despite significant loss, some species are able to persist and flourish in urban settings (McKinney and Lockwood 1999, Shochat et al. 2010). Characterizing how urbanization affects intraspecific traits can help us understand mechanisms promoting species persistence in urban streams. For instance, increased sprint and endurance swimming can ensure survival and persistence of fish in flashy urban streams (Nelson et al. 2015). Plasticity in feeding strategy traits can facilitate survival under the altered food availability conditions of urban streams (Tófoli et al. 2013). Changes in life-history traits can increase fitness of urban stream species (Murphy et al. 2015, Filgueira et al. 2016). For example, Murphy et al. (2015) have suggested that high temperature and high food availability increase the body size of salamanders, which potentially increases their survival and subsequently their fitness in urban streams.

Investigating intraspecific trait change can further help understand the success of invasive species in urban streams. Urbanization increases the occurrence of invasive species in aquatic ecosystems (Havel et al. 2015). Intraspecific trait plasticity of invasive species allows them to take advantage of the urban environments (Davidson et al. 2011). For example, a global meta-analysis suggests that the persistence and proliferation of invasive species in novel aquatic systems is related to traits that enhance food consumption and growth rate (McKnight et al. 2017).

Can we better understand patterns of biodiversity in urban streams?

Explaining observed biodiversity patterns is a central goal in urban ecology because this information can facilitate the management and conservation of species in cities (McDonnell and Hahs 2013). Interspecific trait-based approaches have been commonly used to understand how biodiversity is influenced by urbanization (Evans et al. 2011, Twardochleb and Olden 2016; literature review in Table S2). Such studies typically use average trait data published in the literature to examine trait similarities among species in different assemblages. However, the importance of including intraspecific trait information to clarify mechanisms determining community structure and biodiversity is increasingly recognized (Bolnick et al. 2011, Violle et al. 2012). Including intraspecific information in urban stream studies can clarify links between urbanization, species traits, and ecological interactions that shape community structure, allowing us to better understand the response of biodiversity to urbanization (Bolnick et al. 2011, Verberk et al. 2013, Brans et al. 2017).

Can urbanization cause evolution?

Characterizing intraspecific trait responses allows us to determine if and how urbanization can cause evolution and whether evolution plays an important role in explaining biodiversity patterns of urban ecosystems. Evidence suggests that urbanization has a great potential to drive contemporary evolution and that rapid evolution can be fundamental to prevent species extirpation in rapidly changing environments (Gonzalez et al. 2012, Alberti 2015, Donihue and Lambert 2015, Johnson and Munshi-South 2017). However, to empirically demonstrate that urbanization causes evolution requires establishing a direct causal link between the urban impact on a population, changes in trait distribution, and genetic divergence (Bull and Maron 2016). Recent studies from terrestrial ecosystems are already on this path. For example, Winchell et al. (2016) suggest that large and smooth human-made surfaces, such as concrete, led *Anolis* lizards to evolve longer limbs and more subdigital scales, which improve clinging ability in urban environments. In addition to clarifying evolutionary mechanisms, studying urban systems can help us advance existing evolutionary theory because constraints and trade-offs shaping evolution in urban systems might differ from those in natural ecosystems and current theory might not always be applicable. For instance, classic theory on life-history evolution assumes that nutritional resources are limited, and therefore life-history evolution is mainly shaped by nutritional trade-offs between somatic growth and reproductive investment (Roff 1992, Stearns 1992). However, urban streams are eutrophic and resource rich (Paul and Meyer 2001, Meyer et al. 2005). Increased resource availability might facilitate the consumption of highly nutritious food, which in turn can decouple life-history trade-offs between somatic growth and reproductive investment (Snell-Rood et al. 2015). Research on evolution in urban landscapes can benefit from existing approaches such as breeding experiments and genomic sequencing tools to link urban trait change to trait heritability (Donihue and Lambert 2015, Messer et al. 2016).

Does the functional role of an organism change in an urban environment?

Intraspecific trait changes can alter the role of organisms in the ecosystem. Plastic changes in behavior or physiology can induce nonconsumptive trophic cascades (Ohgushi et al. 2012, Trussell and Schmitz 2012). Evolutionary divergence in life-history traits can change many ecosystem parameters such as nutrient recycling, primary production, and leaf litter decomposition (Bassar et al. 2010, 2012, El-Sabaawi et al. 2015). These ecosystem changes can further alter an organism's traits (i.e., eco-evolutionary feedback; Post and Palkovacs 2009), and it has recently been suggested that urban-mediated intraspecific trait changes can cause such eco-evolutionary feedbacks (Alberti et al. 2017b). However, to empirically demonstrate the existence of these feedbacks, future studies need to couple field observations with both empirical tools, such as common garden experiments, and conceptual frameworks that link trait changes to their ecosystem consequences (Jeyasingh et al. 2014, Travis et al. 2014).

Can we improve biomonitoring approaches in urban streams?

Trait-based approaches are commonly used in biomonitoring assessments. Such approaches often rely on mean trait values calculated across species to infer ecosystem integrity (Zuellig and Schmidt 2012, Nichols et al. 2016). However, within-species variation in traits can be significant, and overlooking this aspect may increase error in biomonitoring assessments. For example, measuring individual body size increases accuracy of size structure estimates, which are an important tool for assessing stream integrity in some situations (Orlofske and Baird 2014). Such improvements can be especially important in monitoring restored urban ecosystems, because biotic assessments are commonly used to infer effectiveness of urban stream restoration practices (Stranko et al. 2011, Bain et al. 2014).

FUTURE CHALLENGES

When characterizing intraspecific trait variability in urban systems, researchers need to choose which traits to focus on. In general, the choice of traits is an important and often controversial issue in all trait-based approaches (Violle et al. 2007). In urban streams, focusing on traits that affect fitness (e.g., body size, growth, fecundity) can be useful for studying questions related to persistence and evolution, while characterizing traits that affect ecosystem function (as defined by Matthews et al. 2011) can be more useful for studying questions relating to trait-mediated ecosystem effects (Fig. 1).

A major challenge when identifying mechanisms that shape the ecology of stream organisms is to isolate agents of trait change. Urban impacts interact and are confounded in streams (Wenger et al. 2009). Multiple agents of stress can lead to additive, synergistic, or antagonistic effects in traits, which can impair our ability to link specific impacts to changes in traits (Schinegger et al. 2016). This challenge could be overcome by combining field research with data modeling and common garden experiments to identify potentially important agents of trait change, test for the effect of specific agents on changes in traits, and assess the strengths of their interactions. For example, in a series of experiments, Coors and De Meester (2008) were able to untangle the additive, synergistic, and antagonistic effects of predators, parasitism, and pesticides on life-history traits of *Daphnia magna*.

It is also important to determine the agents of selection in urban streams, as they will differ from terrestrial systems. Detailed research on how urbanization affects intraspecific traits comes mostly from terrestrial systems. However, terrestrial and aquatic ecosystems are likely to respond to urbanization differently, and it is unclear whether we can extrapolate from one to the other. In terrestrial systems, urbanization is predicted to decrease natural variation in temperature, water, and food availability, which will produce a more stable, uniform environment (Shochat et al. 2006, Alberti 2015). Conversely, urbanization along streams increases the frequency and magnitude of flood events, as well as episodes of nutrient and contaminant addition, which result in a more unstable and unpredictable environment (Walsh et al. 2005, Somers et al. 2013). Therefore, the types of selective pressure in urban streams likely differ from terrestrial urban ecosystems, and an intraspecific approach can highlight differences and generalities between and across the systems, leading to a broader understanding of how urbanization affects communities and ecosystems.

CONCLUSION

With the expansion of cities, there is a growing need to understand the mechanisms through which urbanization affects the biota (McDonnell and Hahs 2013, McPhearson et al. 2016). Here we have identified potential agents of trait change in urban streams and have proposed that intraspecific trait-based approaches can reveal mechanisms of change in these altered ecosystems. This approach should provide important insights into the processes through which organisms respond and adapt to impacts caused by urban development, allowing us to better assess and predict the impacts of urbanization to stream ecosystems.

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