CHAPTER 10

Urbanization and Evolution in Aquatic Environments

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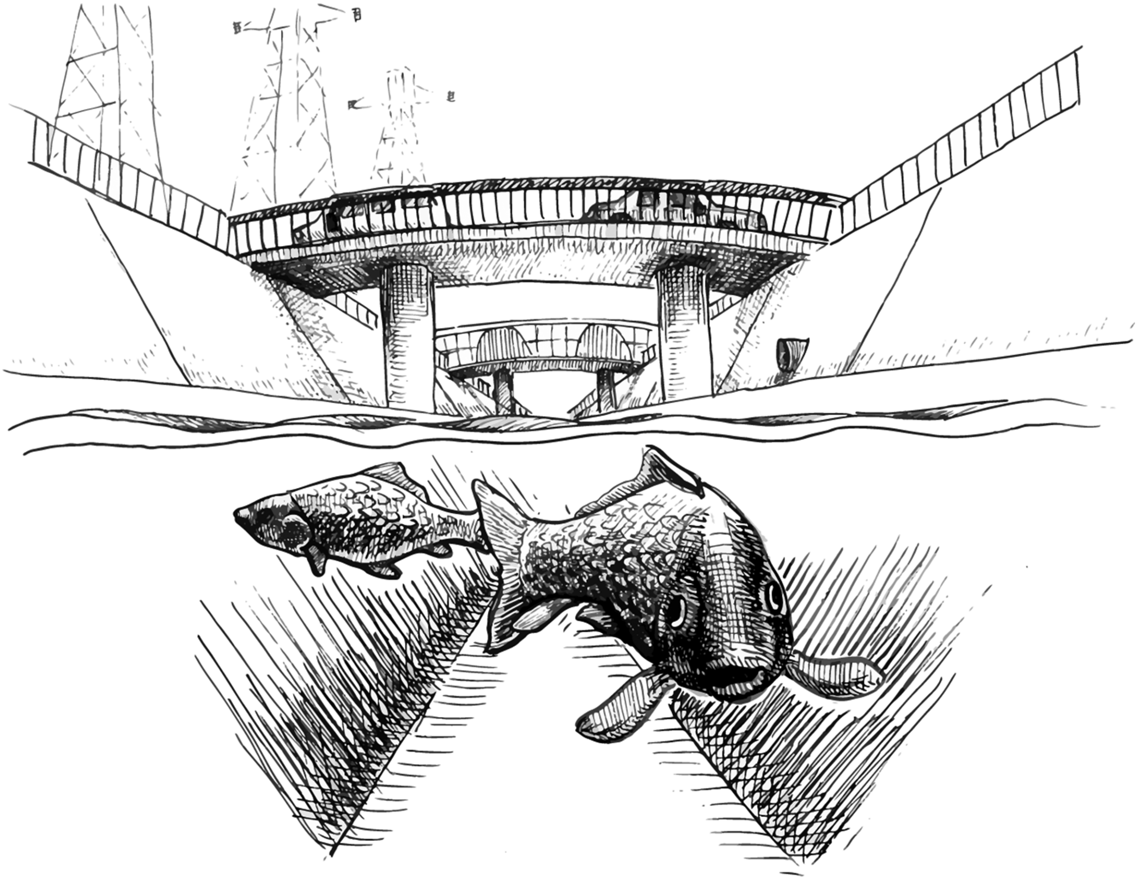

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10.1 Introduction

Throughout the history of our species, we have typically built our settlements, and especially city centres, near water—a pattern that persists to this day (Kummu et al. 2011). This is because of not only the necessity of freshwater for life, but also the utility of water in travel, commerce, food production, security, power generation, and other human uses. Unfortunately, this means that urbanization has had a heavy impact on aquatic species (Vörösmarty et al. 2010). This impact has been well studied from an ecological perspective (Paul and Meyer 2001; Wenger et al. 2009), but the effect of urbanization on aquatic species' evolution is just beginning to be recognized.

Understanding evolutionary responses to urbanization has many practical applications, from human health to pest control to designing sustainable cities (Alberti et al. 2017; Johnson and Munshi-South 2017). Contemporary evolution may affect species persistence, inform conservation decisions, interact with ecological processes and ecosystem services, and even alter how human impacts are gauged. For example, measuring the toxicity of a specific pollutant will lead to inaccurate guidelines if the assayed species is from a population with evolved tolerance (Brady et al. 2017). Owing to the ubiquity of cities, urbanization also presents opportunities to explore evolutionary questions using many replicates and a 'natural experiment' design (e.g., see Chapter 3).

Here we discuss how evolution in aquatic systems is influenced by four major categories of changes that cities can cause: (1) biotic interactions, (2) physical environment, (3) temperature, and (4) pollution. In reviewing evolutionary impacts, we focus on selection, but also discuss genetic drift and gene flow. Along the way, we take into account as many aquatic taxa as possible: plants, algae, invertebrates, fish, and other water-associated organisms (e.g., amphibians, reptiles, and insects with an aquatic larval stage), and we consider all types of aquatic habitats, from backyard puddles to sweeping coastal waters. Despite casting this broad net, we find that research on evolution in urban aquatic habitats is still nascent, with a modest number of truly well-documented cases. We highlight such cases where possible, but in areas where no research has been done, we use theory and empirical studies from other systems to outline testable hypotheses about how evolution might be proceeding (Table 10.1).

The timescale of urban evolution is typically viewed on the scale of years to decades—indeed, the burgeoning research on the topic has largely emerged from studies of contemporary evolution. Consequently, most examples comprise such recent evolutionary change. However, cities first began altering aquatic habitats thousands of years ago. For example, cities of Mesopotamia included large-scale systems of dikes, dams, canals, levees, and gated ditches, causing major alterations to river environments—modifications occurring as early as 5000 years ago. More recently, the Aztecs built their huge city Tenochtitlán on an island in Lake Texcoco, which flourished from 1325 to 1521. The Aztecs heavily modified the aquatic environment, with a large, complex system of canals, causeways, and aqueducts. Thus, city-induced changes to aquatic environments have likely been causing evolution in aquatic organisms for longer timescales than the past several decades. Nevertheless, we inevitably focus on more recent impacts owing to the paucity of studies on longer timescales.

10.2 Biotic interactions

We begin by briefly reviewing the kinds of evolutionary changes that can be caused by disruptions in predator–prey dynamics, competition, and resource–consumer interactions (diet). Urbanization affects these biotic interactions in a myriad of ways: for instance, artificial light can increase night-time predation and alter foraging strategies (Dwyer et al. 2013); pharmaceuticals in urban wastewater affect species' feeding rates (Brodin et al. 2013); and modified structural habitat can alter prey availability and foraging efficiency (Smokorowski and Pratt 2007; Bulleri and Chapman 2010). More directly, urbanization alters biotic interactions by causing the decline or disappearance of sensitive species (especially benthic macroinvertebrates; Brown et al. 2009), introducing non-natives, and increasing the abundance of species that prefer the altered conditions (e.g., when slow-water species colonize a reservoir) (Paul and Meyer 2001).

How species in aquatic habitats respond evolutionarily to urban changes in biotic interactions is

Table 10.1 Major impacts of urbanization on evolution in aquatic species reviewed in this chapter.

Type of urban impact	Types of changes	Likely selection targets
BIOTIC INTERACTIONS		
Predation	Novel predators Loss of predators Changes in predator abundance or behaviour Higher/lower predation pressure	Prey life history, morphology, chemical defenses, anti-predator behaviour
Competition	Novel competitors Loss of competitors Changes in competitor abundance or behaviour Higher/lower intraspecific competition	Foraging and feeding behaviour, body size, trophic traits, diet specialization
Diet	Changes in abundance and diversity of food, consumer behaviour, or foraging habitat Less terrestrial inputs to streams	Broader/narrower niche width, gut length, eye position and morphology, locomotor traits, trophic traits
PHYSICAL ENVIRONMENT		
Habitat fragmentation	Smaller populations More isolated populations Reduced movement distances Altered habitat	Life-history strategies, dispersal traits, body size, locomotor traits, mating system, sexual signals, anti-predator behaviour, trophic traits
Urban stream flow	Increased stream flashiness Higher maximum velocity and variance	Body morphology, fin morphology, body size, swimming performance
TEMPERATURE		
Urban heat island effect	Warmer habitat Longer growing seasons	Timing of spring and autumn events, morphology, body size, pace-of-life syndrome traits, growth rate, thermal tolerance, sex determination
POLLUTION		
Metals/inorganics	Higher concentrations of lead, zinc, copper, cadmium, chromium, arsenic, nickel, and salt	Resistance/tolerance mechanisms
Synthetic organic compounds	Presence of PHCs, PAHs, PCBs, endrocrine disruptors, antibiotics, and pesticides Altered ecosystem productivity Altered chemical signalling	Resistance/tolerance mechanisms
Artificial light at night	Altered light intensity and spectra at night Altered community composition, predator size, and behaviour Disruption of hormone expression	Diel behavioural patterns, movement/migration traits, sexual signals, phenology, endocrine systems, foraging traits, schooling behaviour
Anthropogenic sound	Elevated noise levels Altered frequencies of background sounds	Acoustic signal and receiver traits, endocrine systems, social behaviours, foraging traits, stress response, schooling behaviour
Nutrients and suspended particles	Increased presence of sewage and nitrogen Increased turbidity Lower dissolved oxygen levels Eutrophication Phytoplankton blooms	Toxin resistance, body size, oxygen uptake mechanisms, blood pigments, metabolic rate, visual signal traits

PHCs, petroleum hydrocarbons; PAHs, polycyclic aromatic hydrocarbons; PCBs, polychlorinated biphenyls.

mostly unknown. However, prior work in urban terrestrial systems and the large body of research on evolution in aquatic species allow us to predict how urban aquatic species should evolve in response to altered predation, competition, and diet. We will refer to mosquitofish (*Gambusia* spp.) several times here and throughout the chapter because it has become a model genus for studying rapid and human-induced evolutionary changes.

10.2.1 Predation

Predation strongly influences evolution, with many well-documented examples from aquatic species. To name a few, threespine stickleback, poeciliid livebearing fishes, and crustacean zooplankton have all served as models for how predation drives evolutionary divergence. Although there is not yet enough research for us to generalize how predation regimes affect evolution in urban aquatic systems, it seems reasonable to predict that patterns will probably be similar to those already documented in natural and experimental settings, where predation commonly shapes life histories, morphologies, chemical defences, behaviours, and locomotor abilities.

We offer two pieces of advice to future researchers investigating such predictions. First, an important initial step will be to determine whether the urban population of interest is under higher, lower, or otherwise altered predation pressure. A general pattern of lower predation pressure (and, paradoxically, higher predator density) has been identified among urban vertebrates on land, but hasn't been investigated in the water (Fischer et al. 2012). Importantly, prey often evolve trait changes in response to increases *or* decreases in predation risk from a given source, as well as in response to novel predators and release from predation entirely.

Second, in urban settings, careful study design is necessary to demonstrate that predation, and not some other covarying factor(s), is the driving agent behind the evolution of prey traits. This is because other aspects of urbanization that also influence mortality rates, morphology, behaviour, and life history could be confounded with altered predation regimes. To give just two examples, roadside salt reduces embryonic survival in salamanders (Brady 2012) and both predation and urban light pollution independently affect vertical migration in zooplankton (Gliwicz 1986; Moore et al. 2001). In such situations, model-selection approaches are useful. Research on Bahamian mosquitofish (*Gambusia* spp.) in tidal creeks—where road construction across the creeks has caused dramatic ecological changes that include reduction of predatory fish—has employed model-selection approaches to identify the putative agents underlying phenotypic changes. Changes in predation by piscivorous fishes was found to drive trait changes over ~ 35–50 years in male genital morphology, muscle mass, and fat content, but not male colouration (Heinen-Kay et al. 2014; Giery et al. 2015; Riesch et al. 2015).

10.2.2 Competition

Competition is another strong evolutionary force that can be disrupted by urbanization. A meta-analysis of mostly North American studies indicated that for fish, birds, and amphibians, urban habitats are less densely populated, while macroinvertebrate population densities are higher in urban sites (Sievers et al. 2018). Whether these density changes result in higher or lower competition depends of course on habitat quality and resource abundance, since low densities could just as well correlate with more or scarcer prey. Additionally, competition in urban waters can be affected by altered primary productivity, and for parasites, competition might be affected by increased susceptibility of a host population that is stressed by pollution and warm urban temperatures.

Changes in competition could have several evolutionary impacts. For one thing, competing with novel species can alter selection for traits involved in reducing interference or exploitative competition. Character displacement, where species evolve phenotypic differences to reduce competition for the same resources, should occur when urban conditions increase competition among species. On the other hand, when urban conditions decrease interspecific competition (e.g., extirpation of competitors), this can also lead to changes in traits to better exploit the newly available resources. For instance, as road construction that restricts connectivity between tidal creeks and the ocean has led to reductions of interspecific competitors of Bahamian mosquitofish, their populations have subsequently shown increases in body size (Riesch et al. 2015). Urban environments can affect intraspecific competition as well. Elevated intraspecific competition can lead to the evolution of prey specialization. Bahamian mosquitofish increase individual diet specialization subsequent to anthropogenically induced changes in competition (Araujo et al. 2014).

10.2.3 Diet

In addition to changes in competition, there are many reasons why urban aquatic species might consume different food resources. Urbanization alters the abundance, distribution, and diversity of food, affects consumer behaviour, and modifies the structural habitat consumers navigate while foraging (Smokorowski and Pratt 2007; El-Sabaawi 2018). For instance, urban coastal infrastructure such as breakwaters, jetties, and seawalls support altered epibiota and fish assemblages (Bulleri and Chapman 2010). As another example, urban streams and lakes receive less allochthonous inputs (e.g., terrestrial insects and vegetation fragments) from their immediate surroundings. Such changes can cause dietary shifts. Stable isotope analysis suggests that turtles have different diets in urban settings (Ferronato et al. 2016), while urban freshwater fish consistently eat fewer terrestrial insects and fewer sensitive aquatic insects, relying more heavily on detritus and pollution-tolerant fly larvae (i.e., Diptera) (Francis and Schindler 2009). Not surprisingly, urban diet changes may be taxa-specific. Road construction across tidal creeks has led to altered diets in Bahamian mosquitofish and grey snapper (*Lutjanus griseus*), but in very different manners owing to their different trophic positions (Layman et al. 2007; Araujo et al. 2014).

Dietary changes are notorious for driving evolutionary change, even over short timescales, but specific types of evolutionary changes in urban aquatic species have yet to be described. Some logical areas for hypothesis testing would be evolutionary changes in body size, gut length, trophic morphology, eye position and morphology, and locomotor traits, or changes in the plasticity of these traits. As with other biotic interactions discussed in this section, evolutionary changes caused by dietary shifts in urban aquatic species are a ‘frontier topic’, an understudied area with rich potential for illustrating major ideas in evolutionary biology.

10.3 Physical environment

Urbanization transforms the physical landscape in and around aquatic habitats. While urbanization can greatly modify the structural habitat within which an organism resides (potentially altering its diet, foraging and anti-predator behaviours, and locomotor demands; see section 10.2 and Chapter 12), we focus here on two of the major consequences of urban-induced physical alterations: aquatic habitat fragmentation and disrupted hydrologic regimes. In this section we briefly address how urbanized watersheds impede organism movement and dispersal, and how altered flow regimes are driving evolution in urban streams.

10.3.1 Habitat fragmentation

Barriers that commonly fragment aquatic habitat and interfere with organism movement (reviewed in Fuller et al. 2015) can be quite conspicuous, such as roads, culverts, dams, buried channels, and stream dewatering, while other barriers like thermal pollution (e.g., heated water discharge from manufacturing plants) and wastewater plumes (e.g., treated or untreated sewage fluid moving through waterways) are less visible to the naked eye. Some types of barriers may be surprising, such as artificial night lighting that attracts flying aquatic insects and prevents them from migrating (Perkin et al. 2014) or reduces insect dispersal by affecting larval drift (Henn et al. 2014). Aquatic species that disperse overland, like turtles, amphibians, and some aquatic insects, are also often, but not always, affected by urban habitat fragmentation (e.g., flying aquatic insects can be fatally attracted to polarized reflected light on urban surfaces (reviewed in Smith et al. 2009)). Consequences of a given barrier might be difficult to predict, since closely related species can respond differently to the same barrier: for example, when it comes to travelling upstream through culverts, three crayfish species within a single genus significantly varied in their impedance velocity, meaning the same water speed can be passable to one species but not to a congener (Foster and Keller 2011). To further complicate matters, fragmentation (like other urban changes) can come with a plethora of additional environmental impacts. For instance, fragmentation by roads alone can involve multifarious shifts in selection via changes to runoff patterns, chemical pollution, and light levels, among others (Trombulak and Frissell 2000).

Fragmentation tends to lead to smaller, more isolated populations (although a small proportion of species actually increase in population size or in mobility in urban settings) (Sievers et al. 2018). In theory, since fragmentation decreases gene flow and reduces effective population size, it should increase inbreeding, genetic homogeneity, and genetic drift, while potentially facilitating local adaptation if reduced diversity and drift are not severe (see Chapter 4). To date, many studies have investigated the genetic effects of urban-induced aquatic fragmentation, especially for semi-aquatic organisms, and have overall yielded mixed results: many cases of reduced genetic diversity and increased population genetic differentiation have been uncovered, but this finding is not ubiquitous (e.g., Smith et al. 2009; Mather et al. 2015; Benjamin et al. 2016; Lourenco et al. 2017). It is further important to consider outside factors (such as life history, dispersal ability, small amounts of gene flow, or fragmentation timescale) in such studies of fragmentation effects, as they can have an equal or greater influence on how fragmented populations evolve (Ewers and Didham 2006).

In contrast to the attention on genetic impacts, research on the evolutionary effects of urban aquatic habitat fragmentation on phenotypes is scarce. Theoretically, targets of selection from fragmentation (reviewed in Cheptou et al. 2017) should include life-history strategies (such as those affecting dispersal between fragments), niche shifts (towards more generalist niches or more edge-habitat usage), mating systems (favouring strategies like self-fertilization that are advantageous in small populations), and dispersal traits (although there are arguments for the advantages of both higher and lower dispersal rates). Another possible consequence of fragmentation is altered sexual selection regimes (see Chapter 14). Altered and strengthened sexual selection subsequent to fragmentation has led to enhanced flight performance in damselflies (*Coenagrion puella*) (Tüzün et al. 2017a) and altered male genital shape and the allometry of male genital size in Bahamian mosquitofish (Heinen-Kay et al. 2014).

With the diverse array of possible adaptations and few empirical studies, we are a long way from being able to describe overall trends. However, some existing evidence and hypotheses do point toward future directions in fragmented aquatic systems. For amphibians, it has been proposed that selection in fragmented urban environments should favour 'philopatry, relaxed anti-predator behaviour, and larger body size', since there are fewer predators in isolated urban wetlands and since dispersal into the hostile urban matrix is not likely to result in higher fitness (Munshi-South et al. 2013). For fish, predictions for responses to fragmentation appear to depend on the focal species. In fragmented tidal creeks throughout the Bahamian archipelago, a top fish predator shows narrower trophic niche width (due to decreased prey diversity), while a small, livebearing fish shows a broader food niche (due to higher resource competition) (Layman et al. 2007; Araujo et al. 2014). Such heterogeneity of responses can even occur among close relatives: three mosquitofish species show different kinds of changes in dorsal-fin colouration as a result of habitat fragmentation (Giery et al. 2015). Clearly, expectations for altered selection, and consequently trait evolution, will depend on taxa-specific natural history.

10.3.2 Urban stream flow

Urbanization strongly affects the hydrological regime of many types of aquatic habitat, especially wetlands, stormwater retention ponds, and lotic environments (i.e., rivers and streams) (Jacobson 2011). Owing to their well-documented impacts and relatively clear predictions for altered selection regimes, we centre on urban-induced changes in flow regimes of lotic habitats. One of the most widespread impacts of urbanization on lotic environments occurs via the increased imperviousness of urban land cover. This causes precipitation to reach streams much more quickly, causing water levels to rise and fall sharply. These 'flashy' urban streams have increased maximum water velocity and variance. Flashy streams consequently increase scouring of algal and plant communities, transport nutrients downstream more rapidly, and physically move fauna at a higher rate than less flashy rural streams (Wenger et al. 2009; Jacobson 2011). Notably, not all streams respond by becoming flashy in urban environments: streams in arid areas (surrounded by hardpan) and tropical areas (with already saturated soil from frequent, heavy rainstorms) are flashy by nature, and don't show much difference in flow regime when urbanized (Brown et al. 2009). Very small streams and those in steep drainage areas are also naturally somewhat flashy. Additionally, sometimes human activities reduce flow variability instead of increasing it, as when streamflow is artificially regulated for human purposes. Water levels can also become severely depleted in urban streams and rivers due to diversion for commercial and residential uses in cities.

To date, very few studies have looked at the evolutionary impacts of these dramatic changes in flow regime, but there is evidence that fish respond to flashy urban streamflow regimes by evolving changes in body morphology that affect manoeuvrability or endurance (Kern and Langerhans 2018; Pease et al. 2018) and changes in swimming abilities (Nelson et al. 2003; Nelson et al. 2008; Kern and Langerhans 2019) or swimming plasticity (Nelson et al. 2015) that are related to locomotor efficiency. Both morphology and swimming ability in fishes vary with water velocity in undisturbed systems (Langerhans 2008), so it is likely that these changes in urban fish are caused by altered flow regimes selecting for higher swimming efficiency in fast-moving water. Notably, different fish species exhibit different morphological responses to urbanization—even within the same drainage—apparently reflecting multiple morphological solutions for enhancing steady-swimming performance (Kern and Langerhans 2019). Future work could consider investigating the generality of these findings, the genes underlying fish body shape and locomotor change in urban settings, and hydrological impacts on urban aquatic invertebrates.

10.4 Temperature

Aquatic habitats in cities are often warmer due to the urban heat island effect (see Chapter 6), removal of riparian vegetation, stream widening, water removal, and heated water discharge from treatment plants, power plants, or factories (e.g., Brans et al. 2018; also see Chapter 11). Urban streams and ponds are also characterized by dramatic temporary temperature spikes, brought by stormwater running off hot pavements and other urban surfaces (e.g., Somers et al. 2013). The effect of urbanization on water temperature does, however, depend on local climate—the largest temperature jumps occur when temperate forests are urbanized, while in desert biomes cities may actually be cooler during the day than their natural surroundings (Imhoff et al. 2010). Urban temperatures can strongly influence which aquatic species persist in these settings, and species that can take the heat should experience subsequent evolutionary changes.

There is a sizeable research gap on the evolutionary impact of urban heating on aquatic species, with the notable exception of careful work in the water flea (*Daphnia magna*) by K.I. Brans and colleagues (Brans et al. 2017; Brans and De Meester 2018; see also Chapter 11). However, extrapolating both from these studies and from climate-change research, it seems probable that in urban-tolerant species, traits related to phenology, morphology, size, and sex determination could often evolve in response to urban heating.

10.4.1 Phenology

Few studies have addressed aquatic species' phenological responses to urban heat, although it is known, for example, that the seasonal larval abundance of *Culex* mosquitoes peaks earlier in urban areas (Townroe and Callaghan 2014), and some (but not all) odonates show urban shifts in flight dates (Villalobos-Jimenez and Hassall 2017). Taking a hint from the vast literature on climate change and phenology, we might make a number of predictions: (1) urban heat islands will select for earlier timing of spring biological events and later timing of autumn events; (2) species in middle latitudes might have stronger responses to urban warming than species in tropical zones, due to the former's evolutionary history of reliance on temperature as a phenological cue; (3) small invertebrates, amphibians, and larval bony fishes might have the strongest phenological responses to temperature change; and (4) responses will likely be highly heterogeneous among taxa (Cohen et al. 2018). Each of these predictions is based on phenotypic data: as yet, we know little about how these trends will extend to genetic changes.

10.4.2 Morphology

Increased urban water temperature might have evolutionary consequences for morphological traits. One pathway to this outcome might be through phenology evolution, which has downstream consequences for morphology, size, growth, and predator defences. Another pathway might be through ontogeny: fish morphology can be plastically altered by rearing temperature, and this plasticity has a genetic basis and can evolve (Ramler et al. 2014). There might be an adaptive advantage to certain shape changes associated with temperature: in a latitudinal survey of eastern mosquitofish (*Gambusia holbrooki*), fish with shallower bodies and smaller heads were associated with colder climates (Riesch et al. 2018). Still, there are substantial gaps in research about how widespread such morphological responses are, their plastic vs genetic basis, and whether responses to temperature are parallel across different species.

10.4.3 Body size and pace-of-life

General ecological rules predict that in hotter habitats, smaller species should typically be more successful. In controlled experiments, ectotherms—and especially aquatic species—mature at smaller sizes at higher temperatures (Forster et al. 2012), and in the wild the trend towards smaller sizes with increasing temperatures often holds true on the phenotypic, population, or community level in aquatic bacteria, fish, plankton, and diatoms (Daufresne et al. 2009; Winder et al. 2009; Riesch et al. 2018). This suggests that we might expect selection in hot urban habitats to favour smaller body sizes. Experimental studies have shown that urban *Daphnia* populations do evolve smaller body sizes, which in turn contributes to thermal tolerance (Brans et al. 2017). On the other hand, rotifer and ostracod assemblages in urban ponds do not show a strong effect of temperature on mean community body size (in contrast to cladocerans). This could mean that different taxa will experience different temperature-induced selection, or that for some species, selection for smaller body size might conflict with selection for larger sizes to facilitate adequate dispersal across fragmented urban landscapes (Merckx et al. 2018).

Body size change has received considerable attention in amphibians in an effort to understand the impact of long-term global warming trends. It appears that for this group, size response to temperature varies from one species to another and can sometimes depend more highly on other variables like precipitation, density, or prey abundance, rather than temperature per se (Sheridan et al. 2018). Past studies have mostly focused on decades of frog data under a slowly warming climate, but future research conducted in urban heat islands, where temperatures have risen much higher and faster than overall global warming, might be useful (together with common garden or reciprocal transplant experiments) in predicting future responses of amphibians to climate change.

Predicted smaller body sizes in warmer urban environments are also part of a broader expectation for many organisms experiencing increased temperatures: selection for a faster 'pace-of-life'. The pace-of-life concept is an extension of life-history theory, describing a life-history syndrome, or a suite of covarying life-history traits, where fast-living organisms exhibit rapid growth and maturation, small body size, high fecundity, and potentially reduced lifespan (Debecker et al. 2016). For instance, eastern mosquitofish exhibit a smaller body size, larger reproductive investment, and smaller offspring size in colder environments (Riesch et al. 2018). This fish species is ubiquitous in urban waters, and while temperature can affect phenotypes in both its native and introduced ranges (Ouyang et al. 2018b; Riesch et al. 2018), specific impacts of urban warming have not yet been examined. In *D. magna*, urban populations have evolved faster maturation, earlier release of progeny, and a smaller body size at maturity (Brans and De Meester 2018). These phenotypic changes could prove relatively common in some aquatic invertebrates.

Aquatic insect larvae may often exhibit higher growth rates in warmer urban settings. The larvae of various mosquito species develop faster at higher temperatures and fare better in cities, and this rapid larval development is part of the reason why differences in the incidence of dengue fever (spread by mosquitoes) among neighbourhoods of a major city are explained more by temperature differences than by income level or even human population density (Araujo et al. 2015). This might in turn have implications for virulence evolution. In contrast to mosquitos, damselfly larvae from urban habitats show a genetically based tendency to mature more slowly, possibly because longer growing seasons in warm urban habitats have relaxed selection for fast growth rates (Tüzün et al. 2017b). Considering the well-documented urban heat island effect and the clear-cut predictions in many cases for selection on thermal tolerance, thermal adaptation in aquatic species merits much more attention.

10.4.4 Sex determination

Many egg-laying reptiles and some fish have temperature-dependent sex determination, and at least two studies have shown that sex ratios in snapping turtles and sea turtles can be altered by nest temperature differences caused by shading in urban sites. In these cases, residential vegetation or coastal development actually lowered nest temperatures, resulting in biased hatchling sex ratios (Hanson et al. 1998; Kolbe and Janzen 2002). Temperature-dependent sex determination could often vary between populations with different thermal regimes (for instance, different leatherback turtle populations have different temperature ranges at which males and females are produced) (Chevalier et al. 1999), so it would be interesting to investigate whether urban populations show signs of evolving changes in sex determination. Unfortunately, although the trait of temperature-dependent sex determination can have high heritability, the rate of its adaptive evolution may be too slow in long-lived reptiles to keep pace with urban warming (or even global warming) (Mitchell and Janzen 2010).

The possible evolutionary consequences of anthropogenically altered sex ratios are not clear-cut, partly because the adaptive value of environmental sex determination is rather enigmatic itself. However, this topic is especially important to urban evolutionary biology because multiple aspects of urbanization—temperature, nitrates, pH, and endocrine disrupting compounds—can affect sex determination in aquatic species (Wedekind 2017). We discuss these latter impacts further in the next section.

10.5 Pollution

The effects of pollution on ecology and human health have long been topics of intense research. Perhaps for this reason, evolutionary responses to pollution are fairly well documented compared to other human impacts. This has allowed researchers to delve deeper into this topic, beyond the simple question of '*Do* species evolve pollution tolerance?' and into questions like whether tolerance involves shared mechanisms (Whitehead et al. 2017), how evolution affects persistence (Veprauskas et al. 2018), and the fitness costs that might accompany adaptation to pollutants (Pedrosa et al. 2017). Since urban pollution takes many forms, we divide this section into inorganic pollutants, synthetic compounds, light, sound, and nutrients (thermal pollution is treated separately, under section 10.4).

10.5.1 Metals and other inorganic pollutants

Common pollutants from urban stormwater runoff and atmospheric deposition include a number of metals or metalloids such as lead, zinc, copper, cadmium, chromium, arsenic, and nickel. In regions where road salting is common in winter, salt is another major urban inorganic pollutant. Metal tolerance has been documented in exposed aquatic species too many times to mention here (reviewed in Klerks and Weis 1987), in taxa ranging from fish to algae to isopods to coral to oligochaetes. Since the genetic basis for observed tolerance is not often tested, many questions about the evolution of tolerance remain unanswered, but research in specific areas, like the metallothionein gene and its regulatory regions, has already revealed some common patterns in how metal tolerance evolves (Janssens et al. 2008).

Despite widespread documentation of metal tolerance, sometimes resistance has surprisingly not been found or has even proceeded in the opposite direction. Exposed *Daphnia* actually evolved reduced tolerance to copper and cadmium (Rogalski 2017), possibly due to genotoxic effects of these metals. It is clear that metal tolerance evolution can be fairly complex: duckweed more easily acquires tolerance to some metals over others (Van Steveninck et al. 1992), while in algae, resistance to one metal often confers resistance to another (Hall 1980). Temperature stress interacts with pollution stress (Sokolova and Lannig 2008), as do infectious disease and parasites (Morley 2010), and multiple antibiotic resistances (Sabry et al. 1997). One factor in determining pollution resistance may be genetic diversity, which in turn is itself affected by pollutants (Maes et al. 2005).

The widespread salinization of rivers is generally thought to primarily lead to a shift to salt-tolerant fauna, especially eliminating salt-sensitive insects (Buchwalter et al. 2008). Some fish are capable of adapting to increased salinity (Brennan et al. 2016), and genetic variation in salt tolerance suggests that newts possess at least the raw material needed for evolutionary responses (Hopkins et al. 2013), but the ability of some insects to rapidly adapt to altered salt conditions requires further study (Kefford et al. 2016). There is strong suggestive evidence, supported by a reciprocal transplant experiment, that salamanders in roadside habitats have adaptively evolved to handle saltier conditions than salamanders in neighbouring, unaffected habitats (Brady 2012). Surprisingly, however, amphibians from salt-contaminated pools showed reduced chloride resistance in lab experiments, despite apparent adaptation in the field (Brady 2012; Brady et al. 2017). Additional taxa will need to be studied to decipher the trends and ecological impacts of adaptive evolution to salt in aquatic environments.

10.5.2 Synthetic organic compounds, endocrine disruptors, and antibiotics

An unpleasant assortment of synthetic pollutants are common in urban waters. Runoff from paved surfaces brings gasoline-related compounds (e.g., petroleum hydrocarbons and polycyclic aromatic hydrocarbons), while a broad array of endocrine disruptors, pharmaceuticals, and personal care products easily pass through wastewater treatment plants and enter surface waters around the world (Ebele et al. 2017). Other synthetic organic compounds like pesticides regularly occur in urban water bodies, and an emerging concern is microplastics, which allow persistent organic pollutants to enter aquatic food webs (do Sul and Costa 2014).

What are the evolutionary consequences of these pollutants? Loss of genetic variation is one response (Fasola et al. 2015), since pollution can greatly reduce population sizes or generate a selective sweep. Although other evolutionary responses are not well studied, the immediate biological or ecological impacts of synthetic organic compounds have been documented in a large number of species and systems, and include changes in ecosystem productivity, fish behaviour (aggression, boldness, predation, migration, activeness, social behaviours), insect emergence, and chemical signalling (Brodin et al. 2013; Van Donk et al. 2016; Richmond et al. 2017). The diversity of impacts makes it difficult to generalize or enumerate all the possible changes in selection they could induce. On the simplest level, however, we know that the evolution of resistance can occur: mosquitos (*Anopheles gambiae*) to insecticide (Kamdem et al. 2017); amphipods (*Hyalella azteca*) to pyrethroid insecticide (Major et al. 2018); golden shiners (*Notemigonus crysoleucas*) to the piscicide rotenone (Orciari 1979); and tomcod (*Microgadus tomcod*) and killifish (*Fundulus heteroclitus*) to polychlorinated biphenyls (PCBs) (Wirgin et al. 2011; Whitehead et al. 2017).

Endocrine disrupting compounds (oestrogenic, androgenic, and thyroidal) from human wastewater have been a topic of particularly intense focus. These compounds mimic hormones and have reproductive toxicity in aquatic life, causing vitellogenesis, feminization, and deformities. Models of the evolutionary consequences of disturbed sex determination indicate various potential consequences: the extinction of a sex chromosome, switching to a different sex-determination system (reviewed in Wedekind 2017), or altered sensitivity and reproductive behaviour (Mitchell and Janzen 2010). However, evidence for any of these changes is scant, and researchers have predicted that extinction may be more likely than evolutionary rescue in this situation (Mizoguchi and Valenzuela 2016).

Urban waters often contain a range of antibiotics, as well as bacterial groups carrying and disseminating antibiotic resistance genes (Rizzo et al. 2013). Urban wastewater treatment plants represent the primary source of antibiotics in aquatic environments, and thus regions closest to these point sources often harbour the greatest concentration of both antibiotics and antibiotic resistance genes. The occurrence of antibiotics can drive strong selection for antibiotic resistance genes and antibiotic-resistant bacteria. Urban waters could thus serve as reservoirs for rapid bacterial evolution that can pose serious health risks to humans and animals. Future research is needed to understand the extent and nature of such evolution, its impacts, and ways to mitigate these concerns.

10.5.3 Light pollution

The effect of artificial light at night is an active area of research in ecology and public health. Already several reviews have covered its impact on aquatic and marine ecology (e.g., Rich and Longcore 2006; Gaston et al. 2014). Evolutionary impacts, on the other hand, have largely gone untested (Swaddle et al. 2015; Hopkins et al. 2018), but known ecological impacts point toward where evolutionary forces may be at work.

First, artificial light has well-documented effects on freshwater and marine community composition, predator size and presence, diel activity patterns (i.e., behaviours over a 24-hour period), predation behaviour, and prey assemblages (e.g., Dwyer et al. 2013; Bolton et al. 2017), all of which can have downstream evolutionary consequences (see section 10.2). Altered diel behavioural patterns can particularly influence urban evolutionary trajectories, as these can obviously alter interactions with predators, competitors, resources, and structural habitat, and could even affect hybridization risk, with sympatric heterospecifics typically isolated from one another due to different timings of mating behaviours.

A second mechanism by which light may influence evolution is through sexual selection or changes in reproductive biology. Night lighting disrupts circadian rhythms and hormone production. For example, light can decrease gene expression of gonadotropin, an important reproductive hormone, in perch (*Perca fluviatilis*) (Bruning et al. 2016); change melatonin (which regulates reproduction) levels in carp (*Catla catla*) (Maitra et al. 2013); and affect reproductive biology by causing gene expression changes that lead to ovarian tumours in zebrafish (*Danio rerio*) (Khan et al. 2018). Pheromones are important to aquatic animals and anurans, and artificial light could shape evolution by affecting pheromone-mediated sexual selection (Henneken and Jones 2017), or mate choice and mating efficiency (Botha et al. 2017). How reproductive biology is altered by artificial light may vary by species; for instance, grey treefrogs (*Hyla versicolor*) showed no mating response to light (Underhill and Höbel 2018), while seven other frog species respond to artificial light by decreasing calls (Hall 2016), perhaps a previously adaptive response to increased predation risk on moonlit nights.

Third, light might generate selection for changes in species movement (Gaston et al. 2014), including migration and drift in aquatic invertebrates. Cities could select for non-migrating and non-drifting invertebrates (Rich and Longcore 2006); animals like zooplankton usually migrate at night to avoid fish predation, but if those formerly safe drift/migrate times are now fraught with predators, migration could be selected against. Predation does in fact affect vertical migration in zooplankton (Gliwicz 1986), and urban light pollution decreases vertical migration in *Daphnia*, although whether that is due to predation or is a plastic response to illumination is unknown (Moore et al. 2001).

Besides predation, sexual selection, and movement, there are a host of other studied impacts that might have evolutionary consequences. One such target of selection might be phenology, because artificial light appears to alter biological timings (Gaston et al. 2017) and timings can evolve in some cases; for example, Urbanski et al. (2012) showed rapid photoperiod evolution in an invasive mosquito. Other traits known to be affected by light are foraging, phototaxis, schooling, activity, gene expression, physiology, body condition, and salmon smoltification. Light should probably induce strong selection on endocrine system evolution (Ouyang et al. 2018a) to compensate for negative effects. In some cases, it may not be possible for organisms to adapt to altered light conditions: for instance, if attraction to night lights historically offered fitness advantages, but now yields drastic fitness costs by inducing movement toward artificial lights, and the organism has no sensory means of reliably distinguishing between natural and artificial lights. Future research is clearly needed on this topic.

Finally, it is worth cautioning that even with an increase in data, it will be nearly impossible to formulate general rules about the evolutionary impact of light on aquatic species. Responses to light are highly species-specific, differing dramatically even between closely related species (Bruning et al. 2011), and are highly dependent on ontogenetic stage even within the same species. Depending on ontogenetic stage, fish either avoid light or are attracted to it, and either start or cease various behaviours. The type and colour of the light and duration of its flashes (if any) is also important; for example, the fact that strobe lights deter fish, while mercury vapour lights attract them has been used to direct fish traffic at dams, away from hazardous areas and towards safe bypassages (Rich and Longcore 2006). Type of light matters to amphipod behaviour (Navarro-Barranco and Hughes 2015), and different light wavelengths have different impacts on melatonin production in fish (Bruning et al. 2016).

10.5.4 Anthropogenic sound

Noise from human activities has recently been recognized as a major pollutant and potential evolutionary force (Swaddle et al. 2015). Underwater noise produced by marine resource extraction and seismic surveys (high-decibel blasts in search of oil and gas reserves) causes traumatic injuries and mortality in many species, but we will limit our discussion here to urban noise, such as car and boat traffic and construction. The impacts of noise on animal behaviour and physiology are well documented: immediate effects on fish and frogs have been measured in endocrinological stress responses, metabolic rate change, and behavioural responses such as foraging efficiency, startle response, schooling, and activity level (Kunc et al. 2016); reactions in crustaceans include altered social behaviour, foraging, and predator response (Tidau and Briffa 2016). Noise can have strong negative impacts on fitness, which should influence evolutionary trajectories by diminishing population sizes and/or by selecting for resilient or resistant phenotypes. Since anthropogenic noise infringes on animal communication space, it also has the potential to disrupt acoustic courtship signals, with potential consequences for sexual selection (Amorim et al. 2015). It could even conceivably create a breakdown in reproductive isolation maintained by acoustic mate discrimination. However, to our knowledge, evolution in response to anthropogenic noise has not yet been tested in any aquatic species. Two promising areas of investigation might be (1) stress responses, which have already been shown to be genetically determined and respond to selection in fish, and (2) sexual signalling in anurans, which are known to be affected by traffic noise.

10.5.5 Nutrients and suspended particles

In many cities and especially in developing countries, untreated sewage is a major source of urban water pollution. Worldwide, large cities with inadequate wastewater treatment systems offload prodigious amounts of nitrogen into rivers, sometimes bringing dissolved oxygen levels to nearly zero. Nitrogenous compounds have immediate toxic effects on aquatic life, as well as indirect effects via phytoplankton blooms, eutrophication, and hypoxia (oxygen deficiency) (Camargo and Alonso 2006). Populations can undergo mass mortality before evolutionary responses to nitrogen pollution can arise (there is a good reason why eutrophied coastal waters are termed ‘dead zones’). However, in species that are robust enough to persist, subsequent adaptations to toxins, hypoxia, and turbidity have been observed.

Harmful algal blooms (formerly called ‘red tides’) that follow nutrient enrichment produce high levels of toxins. Evolved resistance to phytoplankton toxins has been documented numerous times in zooplankton (Hairston et al. 2001; Jiang et al. 2011), suggesting it might be widespread. However, resistance in taxa besides zooplankton appears to be either nonexistent or understudied. Interestingly, such toxin resistance seems to have a fitness cost (Dam 2013), which means that in places with seasonal or periodic algae blooms, oscillating loss and gain of resistance could occur regularly.

Adaptations to hypoxia in urban-impacted waters are difficult to predict with certainty. In non-urban scenarios, many species have adapted to low-oxygen environments such as intertidal waters, hypoxic sulfidic waters, swamps, and oceanic benthic zones (e.g., Hoback and Stanley 2001; Bickler and Buck 2007). This gives us some ideas of what kinds of changes might be expected to evolve in anthropogenically impacted waters for a wide variety of taxa (e.g., smaller, thinner bodies and modified gills to increase oxygen uptake; altered blood pigments; lowered metabolic rates). On the other hand, urban environments might complicate matters because organisms must deal with multiple stressors besides hypoxia: for example, in killifish, the evolution of resistance to industrial pollutants comes at the cost of reduced resistance to hypoxia (Meyer and Di Giuliuo 2003).

Another consequence of nutrient pollution, and of the input of fine particles that do not settle to the bottom, can be increased turbidity, which alters the visual communication environment used during mate choice and other visually mediated behaviours. Several examples exist of sexual selection in fish being weakened by turbidity (e.g., Seehausen et al. 1997; Candolin 2009). However, sexual selection can also be enhanced by turbidity in some situations (Sundin et al. 2017), and can lead to increased sexual ornamentation (Dugas and Franssen 2011). Giery et al. (2015) showed that increased turbidity and changes in water colour in Bahamian tidal creeks altered by road construction resulted in changes in male colouration of Bahamian mosquitofish. Turbidity can have other evolutionary effects too, such as morphological divergence driven by altered predator behaviour in turbid environments (Bartels et al. 2012). In light of these findings, it appears that urban-induced changes in turbidity deserve increased attention with respect to rapid evolution related to altered sexual selection.

10.6 Conclusions

To date, the most clear-cut cases of rapid evolution in urban aquatic species come from responses to metals and certain organic compound pollutants, altered temperature, and hydrologic shifts. These anthropogenic factors may commonly drive phenotypic evolution in urban aquatic taxa. Yet, even in these areas, we have gaping holes in our understanding of the predictability, repeatability, magnitude, and frequency of urban-driven phenotypic evolution, and its role in eco-evolutionary dynamics. Building on the existing evidence, additional research in these areas can rapidly begin to address such questions.

A common theme that emerges from our survey is that evolutionary changes are often taxa specific, such that generalized predictions about responses to urbanization may not uniformly apply to disparate species. Even in areas that have received considerable attention (such as evolved metal tolerance or the genetic impacts of urban fragmentation), results have varied across taxa. Predictability of responses may also commonly depend on the ‘scale’ of inquiry—e.g., predictability and parallelism may be greater for whole-organism performance than for morphology than for genes; e.g., a wide range of genetic changes could result in similar performance and fitness values. It is also worth noting that the urban impacts and selective agents we have discussed are not mutually exclusive—they may often influence and interact with one another, as when temperature stress interacts with pollution toxicity.

The clearest take-home message of this chapter is that we direly need more research into the evolutionary consequences of urbanization on aquatic organisms. The urban factors that seem most likely to be affecting aquatic evolution but have so far received very little attention are changes in biotic interactions, fragmentation, artificial light at night, and sound pollution. In each of these areas there is strong evidence for altered selection regimes, and sometimes altered phenotypes, but little-to-no research on evolutionary changes. Since disparate urban factors can influence the same phenotypic traits (e.g., as when both predation and night lighting affect vertical migration in zooplankton), future work may sometimes require sophisticated study design to disentangle the effects of particular selective agents.

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