



# Urban biodiversity management using evolutionary tools

Max R. Lambert<sup>1</sup>✉ and Colin M. Donihue<sup>2</sup>

**Cities are fully functioning ecosystems and are home to no-analogue communities of species that interact with each other and which are subject to novel urban stressors. As such, biodiversity can evolve in response to these new urban conditions, making urban species a moving target for conservation and management efforts. An evolving urban biodiversity necessitates integrating evolutionary insights into management for these efforts to be successful in a dynamic urban milieu. Here we present a framework for categorizing urban biodiversity from a management perspective. We then discuss a suite of example management tools and their potential evolutionary implications—both their opportunities for and potential consequence to management. Urban ecosystems are proliferating but, far from being ecological lost causes, they may provide unique insights and opportunities for biodiversity conservation. Determining how to achieve urban biodiversity priorities while managing pest species requires evolutionary thinking.**

Urbanization is intensifying and expanding worldwide. Human-dominated urban environments—once considered ecological ‘lost causes’—are functioning ecosystems and are increasingly recognized as valuable targets for species conservation and biodiversity management<sup>1–4</sup>. Recent research has demonstrated that the species inhabiting cities are capable of rapidly changing in response to anthropogenic environments<sup>5–7</sup>. For example, the urban heat island effect and urban pollutants have both been implicated in driving animals to rapidly evolve adaptations to urban life<sup>8–12</sup>. Additionally, some aspects of plant reproductive biology have also been demonstrated to evolve in the urban environment<sup>13,14</sup>. The realization that species are capable of quickly evolving in response to urban contexts has driven a flurry of academic and popular interest in urban evolution in recent years<sup>7,15–19</sup>.

Evolutionary insight offers an untapped opportunity to better manage urban biodiversity but also highlights the fact that biodiversity is a moving target in the complex, dynamic urban milieu. Human activities drive the fastest rates of evolutionary change, and those human effects are most pronounced in urban environments<sup>5,20,21</sup>. At the same time, there is an increasing realization that urban areas are important targets for biodiversity conservation and for engaging communities typically underrepresented in the sciences with ecology and evolutionary biology<sup>1–4,22</sup>. Therefore, conservation, evolutionary biology, and community engagement uniquely overlap in urban ecosystems. Given the burgeoning research focus on urban evolutionary biology, the time is right to consider how evolutionary insights can refine urban biodiversity management and conservation efforts.

Conservation and management decisions in urban landscapes can and must account for evolutionary processes. Failure to do so is likely to hinder biodiversity management efforts or result in unintended consequences that include, but are not limited to, target and non-target species declines, wasted funds and labour, or benefits to harmful or pest species (Fig. 1)<sup>21,23</sup>. Here we present a framework for categorizing urban biodiversity from a management perspective. We then discuss a suite of example management tools and their potential evolutionary implications, both their opportunities

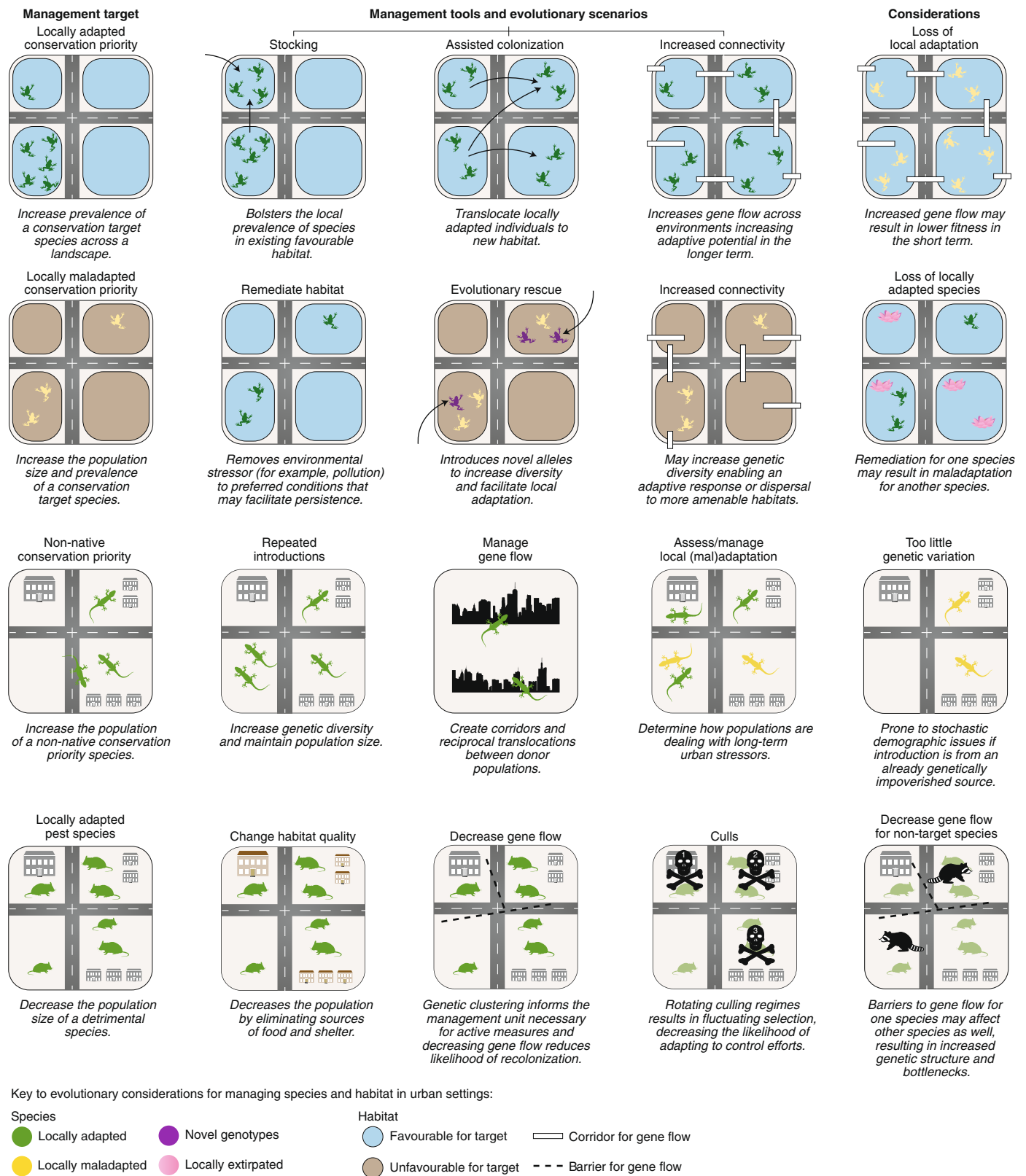
for and potential consequences to management. Our aim here is to bridge the gap between conservation practice and evolutionary biology in urban environments. We hope that this framework can serve as a resource for practitioners and academics to integrate evolutionary considerations into common management scenarios and to guide future research efforts so as to maximize actionable insights for urban biodiversity management.

## Urban communities

Urbanization is both destructive and constructive. In the process of building our cities and suburbs—including constructing green and blue infrastructure or habitats—people alter or eliminate existing habitats and replace them with novel environments. Urban biological communities are largely unintentional assemblages of the native species that persisted during urbanization and the native and non-native species that have since colonized or been introduced (Box 1). This results in unique no-analogue ecological communities: species assemblages that have never existed elsewhere in space or time. Similarly, no-analogue communities resulting from climate change are predicted to produce novel ecological and evolutionary scenarios, complicating conservation and management decisions in protected areas<sup>24,25</sup>. In urban settings, this difficulty in predicting eco-evolutionary outcomes is further exacerbated by the myriad novel stressors and human dimensions inherent in urban ecosystems.

Populations of management target species are nested within broader urban communities; the populations comprising these communities may evolve both in response to different urban pressures as well as to each other. Thus, management decisions affecting one target species will likely cascade to affect other species in the community, but these cascading effects can be difficult to anticipate. Therefore, consideration of the evolutionary history of urban species assemblages (Box 2) and the evolutionary trajectory of urban biodiversity targeted for conservation and management is a research priority. Understanding the evolutionary principles undergirding these interactions and outcomes is the first step in designing effective urban management strategies.

<sup>1</sup>Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA, USA. <sup>2</sup>Department of Biology, Washington University, St Louis, MO, USA. ✉e-mail: [lambert.mrm@gmail.com](mailto:lambert.mrm@gmail.com)



**Fig. 1 | Illustrating potential management tools in multiple evolutionary scenarios for four management targets.** The four management targets are: conservation priority species that are either locally adapted or maladapted, a non-native conservation priority species, and a locally-adapted pest species. Evolutionary insight can guide management decisions that either directly manage populations (for example, various forms of translocations) and/or habitat (for example, enhancing corridors or barriers to gene flow). Initiating an urban management plan can also have evolutionary impacts on other species in the urban community that warrant considerations.

**Box 1 | Urban no-analogue communities**

Urban biological communities are comprised of at least five key categories of organisms that may or may not be the focus of active conservation measures, but whose evolutionary potential may be affected by urban processes and management efforts (Fig. 1). Some species (for example, coyotes or raccoons) may fall within more than one category depending on the context.

**Native**

Desirable, not conservation priorities: we care about these species (for example, acorn ants) because we appreciate native biodiversity and recognize their roles in biological community and ecosystem processes. Studying evolutionary processes can be informative to better manage urban ecosystems to favour these species over ecologically similar but non-native species.

Conservation priority: these are species (for example, western swamp turtle) that are generally of conservation concern and whose ranges might be entirely relegated to urban environments<sup>4</sup>. It is critical to determine the evolutionary processes affecting populations of conservation priority species to tailor management for adaptive states or adaptive processes.

**Introduced**

Neutral: these species (for example, pigeons or clover) are common and typically tolerated. Because we recognize that these species probably play important roles, studying the evolution of these urban species is necessary for understanding the eco-evolutionary processes influencing their roles in urban communities and ecosystem processes.

Harmful: these species (for example, rats) represent threats to human health and property as well as conservation-priority biodiversity. Often our management goals are to minimize the impact and persistence of these species. Understanding harmful species' adaptive states and processes could help us manipulate habitats and populations to minimize their fitness and aid eradication efforts.

Exotic but endangered: Shaffer<sup>2</sup> proposed a novel management option ('urban biodiversity arks') where biologists purposefully introduce and sustain endangered species in urban habitats outside their native ranges. The composition of urban biological communities is often unplanned, however, we have a potential conservation opportunity to encourage species of concern (for example, red-crowned amazon parrots in Los Angeles).

**Evaluating urban evolution**

Evolutionary terminology and concepts (Box 2) are sometimes used colloquially but have more restrictive scientific definitions, sometimes causing confusion. For our purposes here, we have highlighted key evolutionary concepts in two broad research approaches: trait-based studies and population genetics. We note, however, that other areas of evolutionary research like phylogenetics—the study of evolutionary relationships among species—are informative to conservation but are beyond the scope of our discussion here.

**Trait-based approaches.** Populations living in urban ecosystems often differ from rural populations in morphology (for example, body size or limb and head dimensions), physiology (for example, stress hormones, metabolism and pollution susceptibility), behaviours

(for example, phenology, attraction to light, and boldness), reproductive traits (for example, gamete type or quality), and others<sup>5,16,26</sup>. These traits may vary among urban subpopulations or between urban and non-urban populations as a result of evolution or phenotypic plasticity (Boxes 2 and 3).

*Evolution or plasticity?* Trait differences have evolved when those differences are genetically based and heritably passed on to subsequent generations. In contrast, phenotypic plasticity can give rise to trait variation when different environmental conditions alter the expression of the same genotype—an individual organism's particular genetic makeup—in different contexts (Box 3). Unlike evolved trait differences, phenotypically plastic trait variation is generally not heritable because only the environment, not the genetic underpinnings, differs among populations.

These pathways for trait variation are not mutually exclusive: trait variation among populations can be the product of both evolved differences and phenotypic plasticity. One particularly interesting research frontier is investigating the extent to which the capacity of a trait to be phenotypically plastic may itself evolve in urban environments. This scenario has been elegantly demonstrated using ants responding to urban heat islands. Acorn ants, regardless of whether they are from urban or rural populations, can tolerate higher temperatures if raised in warmer rather than cooler environments (a plastic response), but urban ant populations exhibit elevated tolerance of extreme urban heat (an evolved difference) and an increased plasticity in coping with rapid changes in temperatures (evolved plasticity)<sup>11,12,27</sup>.

*Is the trait variation adaptive?* Observed trait variation in populations across urban and rural gradients may or may not confer a benefit in the urban environment. A population's trait expression is considered adaptive if it increases the fitness (higher survival, more offspring) of organisms in that particular ecological context. Trait expression may also be maladaptive, reducing the success of organisms in a particular environment. Or, trait variation may simply be neutral and have minimal positive or negative consequences. Critically, both evolved and plastic trait differences can be adaptive, maladaptive or neutral<sup>28,29</sup>. Moreover, continuing environmental change, including future urban land-use decisions and climate change, could change the adaptive, maladaptive or neutral consequences of an urban population's trait expression, ultimately rendering urban biodiversity management a moving target. Phenotypic variation, whether it be genetic or plastic, can have negative or deleterious effects to individuals.

Observed trait variation—whether due to evolution or to phenotypic plasticity—is sometimes presumed to be adaptive in urban areas<sup>30</sup>. However, we strongly caution against this assumption as, untested, it can lead to overestimation of a species' adaptive capacity and, correspondingly, the impact of conservation and management actions on that species. It remains one of the foremost challenges for urban evolutionary biology research to conclusively determine the plastic or evolved mechanisms driving trait differences in urban populations, but from a management perspective, the need to conclusively distinguish between plastic and evolutionary processes is critical.

**Population genetics approaches.** In contrast to trait-based research, population genetics studies focus on understanding the genetic composition of and variations in gene / allele frequencies among populations. By the numbers, most urban evolutionary studies to date have focused on population genetics<sup>5,7,31,32</sup>. Most urban population genetics studies focus on quantifying neutral evolutionary processes including, for example, population genetic structure, genetic drift, gene flow, inbreeding, genetic diversity and so on (Box 2)<sup>31</sup>. While neutral processes, by definition, do not demonstrate adaptive evolution, insight from population genetics studies has important implications for managing urban biodiversity.

**Box 2 | Evolutionary concepts for urban biodiversity**

**Adaptive:** when a trait conveys a fitness advantage in a particular habitat. Both evolved trait differences (that is, adaptations) and plastic trait changes can be adaptive.

**Maladaptive:** when a trait reduces fitness in a particular habitat. Both evolved trait differences (that is, maladaptations) and plastic trait changes can be maladaptive.

**Local adaptation:** higher fitness of local, genetically based phenotypes over foreign ones due to different selection pressures. An urban population could be locally adapted to the city if urban individuals display higher survival/fitness when reared in the city compared to non-urban individuals transplanted into the city.

**Local maladaptation:** higher fitness of foreign, genetically based phenotypes over local ones. An urban population could be locally maladapted to the city if urban individuals display lower survival/fitness when reared in the city compared to non-urban individuals transplanted into the city.

*Absolute maladaptation:* when a population's mean fitness is lower than its replacement rate, ultimately leading to population decline.

*Relative maladaptation:* when a population's mean fitness is lower than another population's mean fitness. An urban population may be relatively maladapted compared to a non-urban population but its mean fitness may still be equal to or above its rate of replacement, suggesting a relatively stable population.

**Phenotypic plasticity:** non-genetically based phenotypic variation (Box 3). Plastic trait variation could be adaptive, maladaptive or neutral. Myriad studies show phenotypic differences between urban and non-urban environments; it remains an open question as to whether these are genetically based differences or phenotypic plasticity.

*Developmental plasticity:* when a trait's expression is the result of developmental variation among individuals due to being reared in different environmental conditions, rather than genetic differences. Developmental plasticity is typically irreversible.

*Phenotypic flexibility:* when a trait's expression can vary throughout an individual's lifetime due to experiencing different environments or changes in a single environment. Flexible phenotypes are reversible.

**Gene flow:** the movement of genes or alleles (DNA variants of a given genetic region or locus) among populations. Gene flow by itself does not directly reflect dispersal because dispersed individuals may not breed in their new population and therefore do not contribute to gene flow. In urban environments, various landscape features may facilitate gene flow (for example, green spaces, sewers, subway tunnels and road crossings), while others act as barriers (for example, roads and buildings). Gene flow may be endogenously regulated by a given species' natural history or exogenously influenced by anthropogenic actions like translocations or habitat modification.

**Genetic drift:** changes in allele frequencies within a population due to random chance in survival or reproduction. This differs from natural selection which reflects differential survival and reproduction between different genotypes in a given environment. When there is little or no gene flow among different populations, random processes will produce changes in allele frequencies between populations by chance; these changes do not represent adaptation to each populations' particular environment.

**Urban experimental design:** two approaches commonly used in assessing urban evolution are common garden and reciprocal translocation experiments. Common garden experiments take individuals from different populations and rear them in a single environmental condition to assess trait heritability and phenotypic plasticity. Reciprocal transplants involve rearing alternate populations in opposing environmental conditions to assess relative adaptation. For example, rearing urban and rural populations from embryos or eggs in the lab could examine whether an urban trait occurs due to plasticity, evolution, or both. Transplanting the populations (from rural to urban, and from urban to rural) would provide insight on whether any observed trait variability connoted a fitness advantage in either setting. Common garden experiments can, however, demonstrate fitness benefits if organisms are exposed to an isolated urban stressor like pollution or extreme heat as part of the experiment.

**Inbreeding / outbreeding depression:** inbreeding depression occurs when reproduction between closely related individuals results in reduced genetic diversity and increased susceptibility to stochastic processes and future environmental change. The opposite of this is outbreeding depression which occurs when reproduction between more distantly related individuals increases genetic diversity and reduces a population's mean fitness (local adaptation) to its current environmental context.

**Population genetic structure:** genetic variation across time and/or space reflective of dispersal and population boundaries due to physical or behavioural barriers. Population genetics assesses differences in the frequency of alleles that fluctuate within and across populations due to various forces like natural selection, mutation, gene flow and genetic drift. Population genetic structure can reflect ecological processes and evolutionary history and can influence a population's evolutionary potential and trajectory. In urban environments, population structuring may occur at relatively coarse scales (between urban and non-urban environments) and also at relatively fine scales (within an urban landscape) due to different barriers to movement and natural selection to different local pressures.

**Translocation:** a management strategy aimed at moving individuals of a species from one habitat or population to different habitats or populations. Translocations should be informed by source and destination populations' evolutionary histories as well as possible evolutionary consequences. A translocation could take several forms, including stocking to enhance population sizes or genetic diversity of a smaller population, colonizing empty but putatively suitable habitat, or evolutionary rescue, whereby individuals from different populations are introduced to increase genetic diversity to enhance a population's adaptive processes.

For instance, populations with higher genetic diversity should be better able to adapt to future environmental changes overall, including in cities<sup>33</sup>. Therefore, if an urban population of conservation concern was shown to have high rates of inbreeding and low genetic

diversity, management efforts may prioritize introducing new individuals into the population to help bolster that population's adaptive potential against urban stressors. Additionally, understanding rates and directions of gene flow illustrates the extent to which popula-



**Box 3 | Plastic phenotypes in urban environments**

Here, we focus on two forms of phenotypic plasticity: developmental plasticity and phenotypic flexibility<sup>41,42</sup>. We note that other forms of phenotypic plasticity exist, for example, epigenetic inheritance<sup>43,44</sup>, but these forms are difficult to identify and are beyond the scope of our discussion here.

Distinguishing between developmental plasticity and phenotypic flexibility is important for conservation. In particular, developmental plasticity is typically not reversible. This means, for example, that translocating older individuals from a rural population to an urban population may be problematic if the phenotype expressed by that individual is better suited for rural environmental conditions. If developing in urban conditions results in an individual presenting a phenotype that is better suited for those specific conditions, then translocations into various urban habitats may be more effective if they target embryos or young offspring to maximize the chances that a plastically developed trait is best matched to local urban conditions. Phenotypic flexibility, on the other hand, can be reversible and so may facilitate moving organisms at various life stages, including older individuals, if a trait (for example, physiological or behavioural) can adjust to the new conditions at various life stages.

Both forms of plasticity underscore the importance of using common garden and/or reciprocal transplant experiments to determine whether trait differences in urban settings are evolved or plastic (Box 2). Simply measuring trait differences between urban and non-urban populations is necessary but insufficient to determine whether those differences arise from plasticity or evolution, let alone whether that trait variation is adaptive, maladaptive or neutral.

Discerning whether an organism's urban trait arises due to environmentally driven plasticity or evolution is critical to management. If traits enabling a conservation-priority species to persist in the urban environment are due to phenotypic plasticity, conservation practitioners perhaps have a greater number of management tools at their disposal to facilitate the spread and maintenance of that species or to enhance habitat connectivity among urban populations (Fig. 1). However, if this species persists instead because it is locally adapted to urban stressors, then practitioners may be left with fewer management options (Fig. 1).

tions are connected. Gene flow can be a population's 'double-edged sword': on the one hand, gene flow can help a population maintain genetic diversity, but gene flow may also introduce an influx of alleles that are poorly suited for a particular environment (see Case study 1)<sup>23</sup>. Understanding the genetic structure of urban populations is an important step in any conservation and management plan because this information can elucidate biologically relevant management units within the city (see Case study 2)<sup>34–36</sup>.

A review of 167 urban population genetics studies found that urbanization nearly always affects population genetics parameters, but the effects on population genetics are inconsistent across species and cities<sup>31</sup>. While urbanization is often predicted to inhibit gene flow, isolate populations and reduce genetic diversity, this is not always the case. Roughly one-third of studies suggest genetic diversity of urban populations is enhanced by urbanization, in contrast to predictions. For example, urban features like roads or subways can sometimes impede and other times increase gene flow, depending on the species. Because urbanization does not have a single clear population genetics consequence, it is critical for practitioners to account for the biology of target species and the heterogeneity in

local urban environments that might dictate gene flow, genetic drift or population genetic structure before engaging in management activities.

Understanding within- and among-city population genetics can provide crucial context for how urbanization structures biodiversity and facilitates or impedes the movement and success of individuals. Integrating this area of research into management plans will likely enhance the precision and success of urban biodiversity conservation. It is important to note that population genetics and trait-based research are not mutually exclusive. On the contrary, mutual insight from both areas of research will likely provide the most informative guidance for managing urban biodiversity.

**Managing with evolutionary tools**

Making an urban management plan should begin with delineating goals identifying one or more target species, should follow with compiling all available information on evolutionary history (genetic diversity, gene flow, population structure, local adaptation, phenotypic plasticity and so on), and can then be informed by considerations of the intended and unintended evolutionary consequences for target and non-target species. Actively managing urban biodiversity can involve many approaches<sup>4,37,38</sup>, including, for example, remediating low-quality habitat, adding or protecting putatively suitable habitat, or enhancing connectivity among populations either through habitat modifications (for example, under/overpasses or corridors) or via translocations (Fig. 1).

These tools broadly aim to directly manage habitats or populations, with consequences for a species' adaptive state and its adaptive processes (sensu Derry et al.<sup>23</sup>). Managing for an adaptive state means maximizing a population's current fitness and, as a consequence, minimizing phenotypic and genotypic variation. Such an approach may increase fitness in the short term but minimize a population's evolutionary capacity for adapting to future environmental change. Managing the adaptive process of a population means enhancing genetic diversity to promote longer-term evolutionary potential. Managing for the adaptive process may result in maladaptation to current local urban conditions in the short term, but so long as the population is not absolutely maladapted (Box 2), this may be relatively inconsequential for longer-term persistence.

**Managing an evolving urban biodiversity**

One goal of urban management is to bolster existing populations and increase the prevalence of native species of conservation concern or management interest across an urban landscape. If the target species are locally adapted to urban conditions, reducing gene flow from non-urban populations or from different types of urban habitats may be helpful to maintain a particular locally-adapted state. However, doing so may come at the cost of minimizing genetic diversity in urban populations, thereby limiting potential adaptation to future environmental change, urban or otherwise.

Conversely, enhancing gene flow for a locally-adapted population might bolster genetic diversity, enhancing the population's adaptive potential, but with the consequence of reducing its current adaptive state (Fig. 1; locally adapted conservation priority). If the target population is not locally adapted, but is generally plastic to environmental conditions, enhancing gene flow either through translocations or increasing habitat connectivity among urban subpopulations and between urban and non-urban populations may be beneficial for enhancing the urban population's adaptive potential<sup>39</sup>. Alternatively, locally maladapted conservation priority species (Fig. 1; *Locally Maladapted Conservation Priority*) may require mitigating urban stressors to minimize the degree of maladaptation and/or increasing gene flow through population manipulations – such as translocating individuals from other populations – or habitat modification.

## Case study 1 | Pollution and urban frogs

Consider amphibians inhabiting urban stormwater ponds. These ponds are designed to collect stormwater runoff from urban surfaces, and, as such, concentrate myriad contaminants that are harmful to amphibians<sup>45–48</sup>. Nevertheless, research shows that a number of amphibian species—including species of conservation concern—use these ponds regularly, often as readily as they use natural ponds<sup>45,49–52</sup>. One common goal of urban habitat management is to increase green space and connectivity among populations. Yet, in the case of urban stormwater ponds, increasing connective greenspace between ponds may connect a population of a conservation priority amphibian species that is locally adapted to the chemical pollutants in its pond to a rural population or different urban subpopulation that is not adapted to the pollution. The greenspace could thus unintentionally introduce maladapted genes into the pollution-adapted urban amphibian population, to its detriment. However, if amphibians in these communities exhibit plastic responses to pollutants, then increasing connectivity among urban amphibian populations will likely have little impact on pollution susceptibility.

For pest species, managing both adaptive states and adaptive processes are probably key to reducing populations and corresponding detrimental effects (Fig. 1; *Locally Adapted Pest Species*). A pest species that is highly locally adapted to particular local urban conditions may be easier to manage than a pest with extensive phenotypic plasticity. For the first case, it may be possible to change the environment so that population becomes relatively maladapted, but the latter may quickly and flexibly adjust to environmental changes.

Identifying corridors and barriers to gene flow as well as population genetic structure within cities will be important for identifying tractable management units across the urban landscape and for minimizing dispersal that could enhance each subpopulation's adaptive capacity<sup>35,36</sup>. Understanding gene flow is particularly important for determining the best management techniques for pest species.

The species assemblages inhabiting urban ecosystems are largely comprised of the species that persisted during urbanization or have since colonized these environments. Outside of planted species, urban biological communities are largely unplanned species assemblages. One management option to consider would be to “rewild” cities by intentionally reintroducing native species to potentially suitable urban habitats. Doing so would offer an opportunity to experimentally test whether native species that are currently absent from cities are not present because they cannot migrate into built landscapes, because they cannot tolerate urban conditions (e.g. chemical, light or sound pollution) even if they could penetrate cities, or both. For example, experimental work in exurban ponds demonstrated that ponds where wood frogs (*Rana sylvatica*) are currently absent can adequately support these amphibians, suggesting that the developed terrestrial landscape currently limits their colonization of these urbanized ponds<sup>55</sup>. Carefully choosing source populations to rewild cities and suburbs would allow biologists to track the ecology and evolution of those populations that persist. Doing so could enable conservation practitioners to “adaptively” manage urban biodiversity by tracking their changing adaptive states and adaptive processes. To our knowledge, rewilding is not actively employed in urban landscapes – at least not with fauna – but may offer great potential for enhancing native biodiversity in cities.

Shaffer<sup>2</sup> recently proposed taking a rewilding approach one step further, treating cities and suburbs as “urban arks”, i.e. spaces that can help to bolster threatened and endangered species *outside* their native ranges. Selecting urban ark species (Fig. 1; *Non-native*

## Case study 2 | Native and introduced pests

In black widow spiders—a venomous native pest in the southwestern United States—within-city genetic diversity is higher than diversity in rural areas, gene flow and population connectivity is higher among populations within cities, and population genetic differentiation is lower within cities relative to rural areas<sup>53</sup>. Perhaps most importantly, particularly urban subpopulations of black widows act as highly connected hubs that facilitate the spread of urban individuals<sup>54</sup>. In addition to common population and landscape genomic methods, such a network analysis approach may be useful for identifying regions of the city that are central to a pest's persistence and dispersal. While black widow movement may be facilitated generally in cities, identifying and targeting management towards these key hubs may minimize the spread of these pests. For introduced pests, like brown rats, population genetics research has demonstrated substantial within-city variation in population structure, genetic diversity and gene flow<sup>34–36</sup>. This work identifies management units that can be used to focus eradication efforts and identify potential dispersal corridors. Reducing urban habitat quality may also minimize local adaptation, and varying culling techniques across space and time (for example, using different poisons or trapping methods) can also help limit local adaptation in urban populations.

*Conservation Priority*) requires careful consideration about the capacity of these taxa to plastically adjust or rapidly adapt to urban contexts, the likelihood of becoming maladapted (Box 2) to certain urban environments, and if continued introductions or translocations between replicate introduction cities or between urban subpopulations are necessary to maintain adaptive processes.

## Considering the consequences

As with most management activities, manipulating populations or habitat for one target population likely reshapes the ecological and evolutionary processes acting on other members of the community. For instance, improving habitat connectivity to increase gene flow for a target species may also create corridors for introduced pest species to invade new urban habitats (Fig. 1; considerations). This increased connectivity may also have the unintended consequence of eliminating genotypes that have become locally adapted to particular local urban stressors. Additionally, habitat management to minimize dispersal of an introduced pest could have consequences for gene flow in a non-target native species (Fig. 1; considerations).

If a population is locally adapted to a particular urban habitat feature and management remediates this urban stressor, are the consequences for the locally adapted population positive, negative or neutral? The answer to this question is likely specific to a target organism's natural history, the particular urban stressor, and mechanism (for example, physiological or behavioural) experiencing natural selection. In urban stormwater ponds, if amphibians are locally adapted to urban contamination (Case study 1), what happens if pollution entering ponds is cleaned up? Are there costs to being evolved to a contaminant that is no longer present (Fig. 1)? Remediating contamination may ultimately have neutral consequences for the target population; while the urban population may be adapted to contamination relative to non-urban populations, its fitness living in polluted urban water may still be reduced relative to living in the absence of the contaminant. Additionally, while this target species may have persisted in the city because it adapted to contamination, other species may have previously been absent in the city because they were unable to adapt to the contamination.

Remediating contamination may facilitate these other species colonizing urban ponds, perhaps increasing competition with the target species of conservation concern. Under such a scenario, adapting pollution tolerance may facilitate a target species' persistence, in part because doing so minimized competition with other species that could not adapt.

### Towards urban evolutionary management

How do we integrate evolutionary insight into urban biodiversity management? Ideally, managers would define urban management goals and could explore the evolutionary processes that have and continue to shape their target species. This would include assessing genetic diversity, gene flow (rather than just migration), genetic bottlenecks and population genetic structure. This also includes identifying the urban stressors that could limit their target population's success and experimentally testing the adaptive state of the target population to these stressors. Managers could then formulate plans to manage adaptive states or processes in light of the potential evolutionary consequences. Given limitations on time and money, comprehensive genetic and experimental analyses may not be feasible on management-relevant timescales. Even so, a thought exercise (for example, scenarios in Fig. 1) that considers the potential evolutionary processes shaping biodiversity can help identify which urban management decisions would likely help maximize the management success of target populations given uncertainty in existing adaptive states and processes.

Considering evolutionary processes provides a relatively untapped opportunity to improve urban biodiversity management. Sometimes evolution can be useful, facilitating how we manage species of conservation concern and even pests. In other instances, evolutionary dynamics can make management more challenging. We can use evolutionary insight in our urban management practices but doing so entails accurately understanding and communicating the various evolutionary processes shaping the species living in our cities and suburbs. Evolution is also not a conservation panacea: some species will never have the chance to adapt to urban environments, and conservation practitioners may not have the opportunity to assess the evolutionary biology of target species. Considering evolutionary processes offers new opportunities for maximizing outcomes and minimizing unintended consequences for urban biodiversity management.

Using evolutionary ideas to manage urban biodiversity is no small task. Survey research has identified contrasting familiarity with evolutionary principles between conservation practitioners and evolutionary biologists as one of the biggest barriers to effective, evolution-informed conservation<sup>40</sup>. Similarly, academic scientists are unlikely to have the same degree of practical experience as conservation practitioners in urban planning and managing biodiversity and habitat. Effective evolution-informed urban conservation will require a cross-disciplinary approach integrating expertise from conservation practitioners with evolutionary biologists, ecologists, urban planners, social scientists and geographers.

Managing biodiversity in our cities and suburbs necessitates working on many parcels of private property and in relatively dense human communities. This presents numerous challenges but also exciting opportunities for deputizing neighbours into conservation efforts and for tangibly illustrating evolution unfolding right in their backyards. Urban evolutionary biology has not only become a research interest but it has also captured broad popular interest<sup>18,19</sup>. By drawing on evolutionary insights, we have the opportunity to simultaneously improve urban biodiversity management and engage communities with a richer understanding of the evolutionary rules of life.

Received: 27 June 2019; Accepted: 20 March 2020;  
Published online: 11 May 2020

### References

- Dearborn, D. C. & Kark, S. Motivations for conserving urban biodiversity. *Conserv. Biol.* **24**, 432–449 (2009).
- Shaffer, H. B. Urban biodiversity arks. *Nat. Sustain.* **1**, 725–727 (2018).
- Soanes, K. et al. Correcting common misconceptions to inspire conservation action in urban environments. *Conserv. Biol.* **33**, 300–306 (2019).
- Soanes, K. & Lentini, P. E. When cities are the last chance for saving species. *Front. Ecol. Environ.* **17**, 225–231 (2019).
- Donihue, C. M. & Lambert, M. R. Adaptive evolution in urban ecosystems. *Ambio* **44**, 94–203 (2014).
- Alberti, M. Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol. Evol.* **30**, 114–126 (2015).
- Rivkin, L. R. et al. A roadmap for urban evolutionary ecology. *Evol. Appl.* **12**, 384–398 (2018).
- Reid, N. M. et al. The genomic landscape of rapid repeated evolutionary adaptation to toxic pollution in wild fish. *Science* **354**, 1305–1308 (2016).
- Brans, K. I. et al. The heat is on: genetic adaptation to urbanization mediated by thermal tolerance and body size. *Glob. Change Biol.* **23**, 5218–5227 (2017).
- Brans, K. I. et al. Urbanization drives genetic differentiation in physiology and structures the evolution of pace-of-life syndromes in the water flea *Daphnia magna*. *Proc. R. Soc. B* **285**, 20180169 (2018).
- Diamond, S. E. et al. Evolution of plasticity in the city: urban acorn ants can better tolerate more rapid increases in environmental temperature. *Conserv. Physiol.* **6**, coy030 (2018).
- Diamond, S. E. et al. Evolution of thermal tolerance and its fitness consequences: parallel and non-parallel responses to urban heat islands across three cities. *Proc. R. Soc. B* **285**, 20180036 (2018).
- Cheptou, P.-O. et al. Rapid evolution of seed dispersal in an urban environment in the weed. *Crepis sancta*. *Proc. Natl Acad. Sci. USA* **105**, 3796–3799 (2008).
- Gorton, A. J. et al. Little plant, big city: a test of adaptation to urban environments in common ragweed (*Ambrosia artemisiifolia*). *Proc. R. Soc. B* **285**, 20180968 (2018).
- Kern, E. M. A. & Langerhans, R. B. Urbanization drives contemporary evolution in stream fish. *Glob. Change Biol.* **24**, 3791–3802 (2018).
- Schell, C. J. Urban evolutionary ecology and the potential benefits of implementing genomics. *J. Hered.* **109**, 138–151 (2018).
- De León, L. F. et al. Urbanization erodes niche segregation in Darwin's finches. *Evol. Appl.* **12**, 1329–1343 (2018).
- Schilthuizen, M. *Darwin Comes to Town: How the Urban Jungle Drives Evolution* (Macmillan, 2018).
- Koerner, B. I. *How Cities Reshape the Evolutionary Path of Urban Wildlife* (Wired, 2019).
- Hendry, A. P. & Kinnison, M. T. The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653 (1999).
- Stockwell, C. A., Hendry, A. P. & Kinnison, M. T. Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* **18**, 94–101 (2003).
- Li, E. et al. An urban biodiversity assessment framework that combines an urban habitat classification scheme and citizen science data. *Front. Ecol. Evol.* **7**, 277 (2019).
- Derry, A. M. et al. Conservation through the lens of (mal)adaptation: concepts and meta-analysis. *Evol. Appl.* **12**, 1287–1304 (2019).
- Urban, M. C., Tewksbury, J. J. & Sheldon, K. S. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proc. R. Soc. B* **279**, 2072–2080 (2012).
- Merilä, J. & Hendry, A. P. Climate Change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol. Appl.* **7**, 1–14 (2014).
- Alberti, M. et al. Global urban signatures of phenotypic change in animal and plant populations. *Proc. Natl Acad. Sci. USA* **114**, 8951–8956 (2017).
- Diamond, S. E., Chick, L., Perez, A., Strickler, S. A. & Martin, R. A. Rapid evolution of ant thermal tolerance across an urban-rural temperature cline. *Biol. J. Linnean Soc.* **121**, 248–257 (2017).
- Gould, S. J. & Lewontin, R. C. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. B* **205**, 581–598 (1979).
- Hendry, A. P. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *J. Hered.* **107**, 25–41 (2016).
- Littleford-Colquhoun, B. L., Clemente, C., Whiting, M. J., Ortiz-Barrientos, D. & Frere, C. H. Archipelagos of the Anthropocene: rapid and extensive differentiation of native terrestrial vertebrates in a single metropolis. *Mol. Ecol.* **26**, 2466–2481 (2017).
- Miles, L. S., Rivkin, L. R., Johnson, M. T. J., Munshi-South, J. & Verrilli, B. C. Gene flow and genetic drift in urban environments. *Mol. Ecol.* **28**, 4138–4151 (2019).
- Johnson, M. T. J. & Munshi-South, J. Evolution of life in urban environments. *Science* **358**, eaam8327 (2017).
- Munshi-South, J., Zolnik, C. P. & Harris, S. E. Population genomics of the Anthropocene: urbanization is negatively associated with genome-wide variation in white-footed mouse populations. *Evol. Appl.* **9**, 546–564 (2016).



34. Combs, M. et al. Spatial population genomics of the brown rat (*Rattus norvegicus*) in New York City. *Mol. Ecol.* **27**, 83–98 (2017).
35. Richardson, J. L. et al. Significant genetic impacts accompany an urban rat control campaign in Salvador, Brazil. *Front. Ecol. Evol.* **7**, 115 (2019).
36. Combs, M., Byers, K., Himsworth, C. & Munshi-South, J. Harnessing population genetics for pest management: theory and application for urban rats. *Hum.-Wildl. Interact.* **13**, 250–263 (2019).
37. Goddard, M. A., Dougill, A. J. & Benton, T. G. Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol. Evol.* **25**, 90–98 (2009).
38. Hostetler, M., Allen, W. & Meurk, C. Conserving urban biodiversity? Creating green infrastructure is only the first step. *Landsc. Urban Plan.* **100**, 369–371 (2011).
39. Carlson, S. M. et al. Evolutionary rescue in a changing world. *Trends Ecol. Evol.* **29**, 521–530 (2014).
40. Cook, C. N. & Sgrò, C. M. Poor understanding of evolutionary theory is a barrier to effective conservation management. *Conserv. Lett.* **12**, e12619 (2018).
41. Piersma, T. & Drent, J. Phenotypic plasticity and the evolution of organismal design. *Trends Ecol. Evol.* **18**, 228–233 (2003).
42. Martin, L. B., Ghalambor, C. K. & Woods, H. A. *Integrative Organismal Biology* (Wiley-Blackwell, 2015).
43. Brander, S. M., Biales, A. D. & Connon, R. E. The role of epigenomics in aquatic toxicology. *Environ. Toxicol. Chem.* **36**, 2565–2573 (2017).
44. McNew, S. M. et al. Epigenetic variation between urban and rural populations of Darwin's finches. *BMC Evol. Biol.* **17**, 183 (2017).
45. Hale, R., Swearer, S. E., Sievers, M. & Coleman, R. Balancing biodiversity outcomes and pollution management in urban stormwater treatment wetlands. *J. Environ. Man.* **233**, 302–307 (2019).
46. Gallagher, M. T. et al. The role of pollutant accumulation in determining the use of stormwater ponds by amphibians. *Wetland Ecol. Man.* **22**, 551–564 (2014).
47. Brand, A., Snodgrass, J. W., Gallagher, M. T., Casey, R. E. & Van Meter, R. Lethal and sublethal effects of embryonic and larval exposure of *Hyla versicolor* to stormwater pond sediments. *Arch. Environ. Contam. Toxicol.* **58**, 325–331 (2010).
48. Snodgrass, J. W., Casey, R. E., Joseph, D. & Simon, J. A. Microcosm investigations of stormwater pond sediment toxicity to embryonic and larval amphibians: variation in sensitivity among species. *Environ. Pollut.* **154**, 291–297 (2008).
49. Simon, J. A., Snodgrass, J. W., Casey, R. E. & Sparling, D. W. Spatial correlates of amphibian use of constructed wetlands in an urban landscape. *Landsc. Ecol.* **24**, 361–373 (2009).
50. Holzer, K. A. Amphibian use of constructed and remnant wetlands in an urban landscape. *Urban Ecosyst.* **17**, 955–968 (2014).
51. Guderyahn, L. B., Smithers, A. P. & Mims, M. C. Assessing habitat requirements of pond-breeding amphibians in a highly urbanized landscape: implications for management. *Urban Ecosyst.* **19**, 1801–1821 (2016).
52. Holtmann, L., Phillipp, K., Becke, C. & Fartmann, T. Effects of habitat and landscape quality on amphibian assemblages of urban stormwater ponds. *Urban Ecosyst.* **20**, 1249–1259 (2017).
53. Miles, L. S., Johnson, J. C., Dyer, R. J. & Verrelli, B. C. Urbanization as a facilitator of gene flow in a human health pest. *Mol. Ecol.* **27**, 3219–3230 (2018).
54. Miles, L. S., Dyer, R. J. & Verrelli, B. C. Urban hubs of connectivity, contrasting patterns of gene flow within and among cities in the western black widow spider. *Proc. R. Soc. B* **285**, 20181224 (2018).
55. Shepack, A. et al. Species absence in developed landscapes: an experimental evaluation. *Landsc. Ecol.* **32**, 609–615 (2017).

### Acknowledgements

We thank B. Rosenblum, T. Jenkinson, O. Hernández-Gómez, M. Womack, M. Grundler, A. Rothstein, A. Byrne, K. Klonoski and C. Noss for providing critical feedback on this manuscript. The ideas in this manuscript benefited from conversations with M. Alberti, E. Carlen, S. Des Roches, K. Dyson, T. L. Fuentes, L. Guderyahn, G. B. Pauly, C. E. Santoro, C. J. Schell, O. J. Schmitz, H. B. Shaffer and I. Wang. We thank B. Verrelli for feedback that improved this manuscript.

### Author contributions

M.R.L. initiated the project. Both authors contributed to the writing and editing of the manuscript.

### Competing interests

The authors declare no competing interests.

### Additional information

Correspondence should be addressed to M.R.L.

Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints).

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© Springer Nature Limited 2020