Multifaceted mechanisms of metropolis: Integrating society, ecology, evolution, and plasticity (SEEP) to advance urban evolutionary ecology

1. Statement of Need

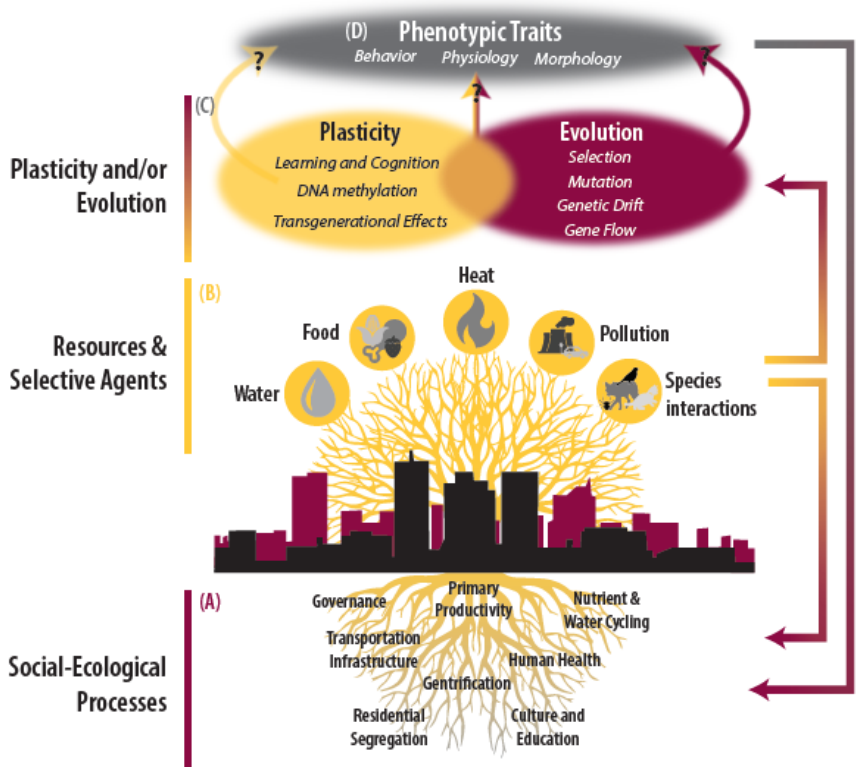
Urbanization produces rapid and often extreme shifts in the environmental conditions to which organisms are exposed (Grimm et al. 2008). Even when landscape structure is similar to surrounding wildlands, such as in remnant patches of native vegetation or yards with native landscaping, heat-island effects and human-subsidized resources often result in altered ecophysiological conditions, which can be either disruptive or beneficial to organisms. Although some of these outcomes are increasingly well documented, large gaps remain in our understanding (Johnson & Munshi-South 2017; Szulkin et al. 2020; Miles et al. 2021). *A prominent outstanding question centers on the extent to which the success of some urban species is the product of pre-existing plasticity, local adaptation to the new environment, or the evolution of novel plastic responses.* This question remains unanswered in most urban systems (Alberti 2015; Rivkin et al. 2019; Alberti et al. 2020; Des Roches et al. 2021; Lambert et al. 2021), but is central to the emerging study of eco-evolutionary dynamics (Hendry 2016). Indeed, understanding these non-exclusive mechanisms, which operate at different temporal scales, is critical to our understanding of the determinants of an urban organism's performance, urban population growth, and the basis of urban ecosystem biodiversity (Martin et al. 2019; Des Roches et al. 2021). In addition, investigating the mechanisms that shape wildlife responses (e.g. ecological, evolutionary, behavioral, physiological) to urbanization and people is crucial for mitigating future human-wildlife conflicts that jeopardize efforts to sustain biodiversity. Synergistic and inclusive frameworks that integrate well-being and equity for both human and non-human populations will be necessary for advancing positive ecosystem outcomes and social-ecological solutions.

We propose a workshop for Spring 2022 that focuses on the intersection of evolutionary biology, physiological, and behavioral ecology to ask ***to what extent do organisms respond to the altered climate and resource availability of urban areas via phenotypic plasticity, genetic adaptation, and/or the evolution of adaptive plasticity?*** This workshop will hone our mechanistic understanding of the genetic, physiological, and behavioral mechanisms that scale up to population- and community-level changes in the abundance and distribution of animals in metropolitan regions, as well as the human drivers, outcomes, and feedbacks that shape these changes across heterogeneous urban landscapes and over time (**Fig. 1**). Our focus on mechanistic drivers will center on five human-altered resources and selective agents associated with urbanization: **heat, food, water, pollution, and species interactions**. These urban factors can interact to produce complex biotic and abiotic outcomes at individual, population, and community levels. In addition, these resources/selective agents are distributed heterogeneously within and across cities as a function of both contemporary human decisions (Cook et al. 2012) and past legacies of racism and other social processes (Larson et al. 2017; Schell et al. 2020; Des Roches et al. 2021). Thus, a complete understanding of eco-evolutionary dynamics in urban systems requires examination of the social (human) processes shaping animals' exposure to altered resources and selective agents, as well as potential feedback via human interactions with wildlife (**Fig. 1**).

We will apply this framework to the case study of the Central Arizona Phoenix Long Term Ecological Research site (CAP LTER). The workshop will seek comparisons among taxonomic groups, with an emphasis on animals (e.g. birds, mammals, arthropods), given the expertise of our organizing team, but with the full ability to inclusively examine this framework in plants and other organisms, especially given CAP LTER's rich plant database (Allen et al. 2018; Childers et al. 2018). Using a trait-based approach (Lambert & Donihue 2020; Szulkin et al. 2020), we will identify common phenotypic and genotypic traits across taxa and spatio-temporal scales that are ideal for investigating fundamental evolutionary dynamics in the urban landscape. Some potential fitness-linked traits to examine include presence/expression of genes involved in thermal tolerance, heat shock proteins, processing of fatty and carbohydrate-rich foods, or osmoregulation, as well as behavioral traits such as boldness or avoidance/use of human-provided resources. This trait-based approach will facilitate connecting altered biotic

communities to ecosystem services and effects on human well-being (Larson et al. 2019; Brown et al. 2020; Andrade et al. in review). Funding from the DCL-LTER evolutionary biology program will facilitate the identification of the most feasible traits and study systems to pursue in future work, as well as preliminary analyses of existing datasets, using the CAP LTER as a case study.

Fig. 1. SEEP conceptual framework incorporating evolutionary processes in LTER research in an urban social-ecological system. (A) Human-impacted ecological conditions in the urban environment shape the direction, strength, and spatiotemporal distribution of **(B)** resources and selective agents (e.g., ***heat, food, water, pollution, and species interactions***) experienced by nonhuman organisms. **(C)** These selective pressures can lead to phenotypic plasticity (within generations), genetic adaptation (across generations), and/or the evolution of adaptive plasticity. **(D)** Whether observed phenotypic traits (e.g., behavior, physiology, and/or morphology) are the result of plasticity, genetic adaptation, or adaptive plasticity, however, remains an outstanding and central question for advancing our understanding of the mechanisms contributing to urban adaptation (D). Evolutionary and phenotypic outcomes may necessarily feed back to alter human social systems across a variety of scales, from individual community members and property managers to institutional-level policies.



We have identified a diverse team of organizers and propose holding a workshop that will examine how CAP LTER data, samples, and sites can best be harnessed to address the question of plastic and evolutionary changes in traits that respond to urban heat, food, water, pollution, and species interactions. CAP LTER is an ideal model system for integrating evolutionary biology into LTER research, as CAP scientists are at the forefront of developing mechanistic understandings of the ecological, physiological, and behavioral adaptations of organisms to city life (Sepp et al. 2018, 2020), and CAP is also a long-time leader in developing innovative and integrative approaches to social-ecological research (Childers et al. 2015; Grimm et al. 2017; Groffman et al. 2017; Pickett et al. 2017). CAP has amassed long-term datasets encompassing biotic community data (Bateman et al. 2017; Warren et al. 2019), ecophysiological studies of single species (Davies et al. 2016; Cook et al. 2017), environmental data (Childers et al. 2018; Brown et al. 2020), surveys of food and water resources (Childers et al. 2018), land-use and land-cover change (Zhang & Li 2017), and neighborhood-based social

surveys (Larson et al. 2019). In addition, long-term sample collections for some taxa (e.g. plants, arthropods) may facilitate analyses of changes in phenotypic and/or genotypic traits in urban populations.

There are several key challenges to pursuing a greater integration of urban evolutionary approaches. In particular, an expansion beyond existing CAP scientists' expertise is necessary to grapple with the central question of evolutionary and plastic mechanisms. The proposed workshop leadership team and participant list adds external leaders in urban evolutionary and physiological ecology to an existing team of CAP scientists. This knowledge of evolutionary and physiological ecology will complement expertise at multiple levels of biological organization and with social science to address human-wildlife interactions as well as human well-being and social-ecological feedback loops. Identifying new and additional datasets and analyses will be required to explicitly measure changes in phenotypic and genotypic traits. To address this combination of strengths and challenges, the workshop funding will support:

- Intellectual exchange among existing CAP scholars and emerging leaders in the field of urban evolutionary biology to develop and refine research questions
- Information-gathering on existing data and archived samples and their potential utility in measuring long-term changes in genotypic and/or phenotypic traits
- Pilot analyses of population changes and resource inputs to develop hypotheses about anthropogenic resources and selective agents
- Defining a unified research agenda for collaborators with complementary expertise (i.e. selection of one/few target study systems), to pursue linking LTER data with mechanistic studies
- Identifying potential companion cities (e.g. Twin Cities (MSP) LTER) for cross-site comparisons
- Strengthening local and national community-engagement efforts through immersive K-12 and undergraduate research experiences and media (e.g., podcast series)

2. Organizing Committee

The workshop will be produced and moderated by an organizing committee, chaired by PI Kevin McGraw. Currently, the organizing committee of 6 members (see below) combines leadership in the CAP LTER community, including from its home institution (Arizona State University) and outside partners, as well as key external leaders in the field of urban evolutionary biology (Diamond and Martin). This diverse group has expertise spanning many taxa, ranging from birds to mammals to arthropods, and with complementary approaches to studying traits in urban organisms (e.g. genetic, behavioral, ecological, community) as well as human activities, actions, and outcomes. Four members of this group (McGraw, Warren, Johnson, and Schell) were central players in the organization and delivery of our preliminary CAP workshop on Urban Heat, Food, and Water in January 2020. We plan to expand the committee membership, adding expertise in the session themes and in environmental-justice issues.

The committee chair will coordinate the logistics and communications for the workshop. PI McGraw is based at the ASU Tempe campus and is embedded in the necessary administrative networks to facilitate on-site planning. The committee members will be responsible for jointly creating the detailed agenda for the workshop, selecting and inviting speakers and participants, and designing the website with support from the graduate research assistant. The perspectives and social networks of the full committee will be harnessed to ensure the workshop messaging and targeted invitations result in a diverse panel of speakers and other participants.

Committee chairperson:

- **Kevin McGraw (lead PI), Arizona State University**, CAP LTER scientist. McGraw is a behavioral ecologist and physiologist in the School of Life Sciences (SOLS) at ASU and focuses on the impacts of urbanization and specific human activities (e.g. bird feeder use/cleanliness) on the health, nutrition, behavior, and sexual signaling systems of locally abundant songbirds in Phoenix, AZ. McGraw is also Associate Director of Facilities in SOLS, which will permit direct administrative oversight of on-site meeting arrangements and logistics at ASU.

CAP LTER members:

- **Chad Johnson (co-PI), Arizona State University**, CAP LTER scientist. Johnson is an urban behavioral ecologist who has been studying the effects of urbanization on arthropod behavior, ecology, and evolution for 15 years. In particular, his group has focused largely on black widow spiders as urban pests, asking whether phenotypic plasticity promotes their success in cities.
- **Paige Warren (co-PI), University of Massachusetts-Amherst**, CAP LTER scientist. Warren is an urban ecologist with over 20 years' experience of working with CAP LTER and extensive experience leading interdisciplinary research teams. Her work examines the social-ecological dimensions of urban biodiversity, avian community ecology, and trophic dynamics.
- **Chris Schell (co-PI), University of California Berkeley**, CAP LTER scientist. Schell is an urban evolutionary ecologist and behavioral biologist who has studied the organismal consequences of human-carnivore interactions for the past 9 years. His recent works articulate the consequences of systemic racism on urban biodiversity, as well as advancing justice, equity, diversity, and inclusion (JEDI) in ecology and evolution disciplines.

Members external to CAP LTER:

- **Sarah Diamond (co-PI), Case Western Reserve University,** Diamond is an evolutionary ecologist with expertise in physiological trait variation, plastic and evolutionary mechanisms, and responses to global climate change and urbanization.
- **Ryan Martin (Senior Personnel), Case Western Reserve University,** Martin is an evolutionary ecologist whose research focuses on how biotic interactions and environmental variation drive natural selection and how plasticity and evolution interact during adaptation to changing environments.

Proposed external members (*goal of at least 2 additional members*):

- **Ann Charmantier, Centre d'Ecologie Fonctionnelle et Evolutive (France).** Charmantier's work examines intraspecific variation of life-history, morphological, and behavioral traits in natural populations, emphasizing the role of environmental degradation in driving variation in these characters.
- **Simone Des Roches, University of Washington.** Des Roches studies intraspecific variation, eco-evo dynamics, and rapid adaptation is a wide variety of taxa. She is an early-career scholar and emerging leader in studying how human society impacts eco-evo dynamics.
- **Nyeema Harris, University of Michigan (invited).** Harris studies the role of species interactions in eco-evolutionary dynamics, with a focus on mammalian communities and their parasites. She is a leading voice in calling attention to racism in the fields of ecology and evolutionary biology and promoting a need to address environmental justice in eco-evolutionary research.
- **Jessica Hua, Binghamton University.** Hua's research examines the mechanisms shaping ecological interactions, evolutionary processes, and eco-evo feedbacks, with a focus on the evolution of plasticity in response to environmental pollutants and toxins.

Proposed CAP social science/environmental justice members (goal of at least 1 additional member):

- **Fuschia Ann Hoover, UNC Charlotte (invited).** Hoover is an early-career, interdisciplinary scholar with expertise in green infrastructure performance and environmental justice and equity.
- **Jose Rosales Chavez, Arizona State University.** Rosales Chavez is an early-career anthropologist and new member of CAP LTER with expertise in food security, access to food, health outcomes, and social determinants of health.
- **Kelli Larson, Arizona State University.** Larson is an environmental geographer and leader in CAP LTER. She coordinates the long-term social survey data collection at CAP, and has expertise in ecosystem services/disservice, water resources, and human-wildlife interactions.

3. Relevant Recent Meetings

The topic of urban eco-evolutionary dynamics has been brought to prominence in part through a recently published edited volume on urban evolutionary biology (Szulkin et al. 2020) as well as symposia

at recent conferences of several national and international scientific societies (listed below). The PI and co-PIs have participated as organizers or presenters in all but one of these 7 symposia. *Our proposed workshop builds on these meetings in identifying a specific evolution-focused research agenda grounded in LTER data and by incorporating greater integration of social science and environmental justice*.

a) CAP LTER Heat/Food/Water workshop (McGraw and Warren, co-organizers; Johnson and Schell, participants) – 16 January 2020: Arizona State University, Tempe, AZ. This preliminary one-day meeting, centered on behavior and ecophysiology, involved a small group of 25 participants, most of which were CAP scientists, in addition to three outside participants and a community partner. Co-PI Schell was an invited external participant at that workshop, and in 2021, he formally joined CAP LTER. An emergent theme from this workshop was the need to expand our scope by including a strong evolutionary focus and direct tie-ins to CAP LTER's long-term samples and data. Thus, the proposed workshop will greatly expand the number of external participants and will explicitly focus on evolutionary biology, through the co-leadership of co-PIs Diamond and Johnson and Martin (senior personnel).

b) ABS/Behaviour 2019 (Johnson: organizer; McGraw: invited speaker) - *Animal behavior on an urbanized planet*. University of Illinois, Chicago, July 23-27, https://www.animalbehaviorsociety.org/2019/program-symposia.php

c) IOC 2018 (no participants from our leadership team) - *Pre-symposium: Avian urban ecology: Behavioral and ecological consequences of urban life across the globe.* Vancouver, Canada, August 19-26. https://eounion.org/latest-news/avian-urban-ecology-behavioral-ecological-consequences-urban-life-across-globe/

d) Joint Congress on Evolutionary Biology 2018 (Diamond: invited speaker) - Symposium: Evolution in an urbanizing world, Montpellier, France. August 18-22. https://eseb.org/wp-content/uploads/2018/08/2018_Program.pdf

e) SICB 2018 (McGraw: invited speaker) - *Symposium: Behavioral and physiological adaptation to urban environments*. San Francisco, CA, January 3-7. https://sicb.burkclients.com/meetings/2018/symposia/urban.php

f) Evolution 2017 (Martin: invited speaker) - *Symposium: Evolution in urban ecosystems.* Portland, OR. June 23-27. http://www.evolutionmeetings.org/uploads/4/8/8/0/48804503/final_evol2017_program.pdf

g) 19th New Phytologist Workshop 2017 (Diamond: invited speaker; Martin: invited participant). *Synthesis in the City: Urban Evolutionary Ecology.* University of Toronto Mississauga, July 27-30. https://www.newphytologist.org/workshops/19

4. Intellectual Merit

The workshop will advance a new framework for integrating **s**ocial, **e**cological, **e**volutionary, and **p**lasticity processes (SEEP framework, **Fig. 1**) for understanding the complexity of animal responses to urban systems and how these responses feedback to influence human-wildlife interactions. Our framework highlights the importance of the DCL-LTER evolutionary biology program call for workshop funding. The intuitive, yet powerful, premise here is that there is a reciprocal feedback loop wherein human actions shape the urban ecosystem, which in turn affects the humans living in that ecosystem. While historically this work has focused on the interaction between humans and the abiotic factors of urban environments (e.g. supplemental water use, urban heat islands; Kim 1992), more recently researchers have focused on organismal-level questions about urban ecosystems (Ouyang et al. 2018). Specifically, how do human decisions affect urban biodiversity (Dearborn & Kark 2010; Avolio et al. 2018; Lambert & Donihue 2020)? How do human decisions affect the population growth of urban animals (Narango et al. 2018)? How do human decisions change the selection regimes that urban plants and animals experience (Yeh 2004; Irwin et al. 2013, 2018)? And most recently, what are the principal factors contributing to rapid adaptive and neutral evolutionary processes in these urban environments

(Miranda et al. 2013; Diamond & Martin 2021)? In each case, the question is twofold: how do humans affect the biotic and abiotic components of urban ecosystems, and what are the reciprocal consequences for human-wildlife interactions, ecosystem services, and coexistence in cities? CAP-LTER is positioned to address these questions as a leader in disentangling the complexities of social-ecological drivers that shape urban ecosystems (the SE in SEEP; Grimm et al. 2000; Childers et al. 2015; Grimm et al. 2017; Groffman et al. 2017; Andrade et al. 2021). However, adding a strong evolutionary component to LTER data sets generally, as well as to the CAP-LTER research specifically, is critical to predicting how these coupled human-natural systems will change over time. As we argue below, urban eco-evolutionary dynamics are complex and must be integrated into the study of urban ecology to begin to fully grapple with the complexity of the ecosystems we are creating and expecting to inhabit (Alberti et al. 2020). Lastly, we suggest that an understanding of an organism's performance in urban settings (e.g. physiology of urban heat stress/tolerance, behavioral shifts associated with novel urban food sources or urban predators) is essential for integrating principles from urban ecology with evolutionary processes in cities.

4.1 Why mechanism matters: disentangling plastic from evolved responses to urbanization

Phenotypic changes in response to urbanization can be driven by plastic and evolutionary responses. Determining the specific mechanisms that underlie these responses is critical, as they can operate over different timescales and under different constraints (Diamond & Martin 2020). For example, plastic responses are possible within generations, whereas evolutionary responses, even over contemporary or rapid timescales, necessarily occur across multiple generations. Although historically, evolutionary responses to contemporary environmental changes such as urbanization were thought to be exceptional and rare, there has been a paradigm shift in the field, lending increasing support to rapid evolutionary responses over mere decades rather than over deep time, i.e. thousands or millions of years (Alberti et al. 2017). Indeed, both plasticity and evolution appear to contribute to many responses of populations as they undergo the urbanization process (Diamond & Martin 2021).

While there is a growing appreciation that disentangling plastic from evolved responses to cities is an important task, in fact, these two mechanisms can interact with one another in complex ways (Diamond & Martin 2016). Specifically, plasticity can facilitate evolution by buying time for evolution to occur or by providing the raw variation upon which selection can act via novel gene-by-environment interactions. Indeed, initially maladaptive plastic responses to urban environments could even speed the rate of contemporary evolution (Ghalambor et al. 2015). By the same token, plasticity can impede adaptive evolution by buffering populations from selection pressures in cities, and plasticity can itself evolve in response to altered selection pressures (Ghalambor et al. 2007).

Trait-based approaches may be useful in determining how, why, and which populations are more likely to evolve or more likely to rely solely on plasticity (Diamond & Martin 2020). For example, local adaptation to urban environments might be swamped by gene flow in highly dispersive species, resulting in a dominant role for adaptive plasticity. Even for species that rely predominantly on evolutionary change to respond to urbanization, plasticity remains the faster timescale response, and thus could have differential effects on urban eco-evo dynamics. Finally, phenotypic changes in response to urbanization may not always be adaptive or promote population persistence (Diamond & Martin 2020). Urbanization, by imposing barriers to gene-flow and habitat fragmentation, could cause non-adaptive evolution via drift, and novel environmental stressors may reveal novel maladaptive plasticity. Scaling up from these individual species responses and the plastic and evolutionary mechanisms that underlie them might help to reveal and forecast broad-scale biodiversity responses to urbanization, with further implications for ecosystem functioning in cities (Thompson et al. 2021). This is where the leveraging of long-term datasets such as CAP LTER become important as they allow us to understand signatures of urban effects on populations and communities and couple these patterns with directed experiments to disentangle their mechanistic basis. These distinctions are critical for developing future predictions and thus guiding urban management and planning decisions.

5. Meeting the challenges of integrating evolutionary biology in an LTER

We will tackle two critical questions when considering the integration of evolutionary biology with LTER data - what types of data are needed to address eco-evolutionary dynamics, and to what extent does the LTER network, and especially CAP, already have those data? From an evolutionary biologists' perspective, long-term measurements of traits or collections of biological samples could address questions surrounding phenotypic variation and non-adaptive processes like drift, gene flow, and mutation rate (Miles et al. 2019). For example, mutation rates could be examined using historic samples to ask how population genetics/genomics changes over time. Signatures of genomic selection could also be examined. We acknowledge, however, that countergradient variation would manifest as a lack of trait variation across urbanization gradients, but underlain by genetic changes in populations. These analyses and data can set up hypotheses for future research. To examine plastic and/or evolved responses, phenotypic data need to be paired with experiments (e.g. common garden). To the extent that previous explorations of trait variation are available, genetic/genomic data of extant populations coupled with historic trait data could also address the relative importance of plastic and evolved responses. Assessing the adaptive nature of responses requires assessing fitness, ideally via experiments to examine both adaptive plasticity and adaptive evolution. Adaptive explorations are, of course, separate from whether or not there is a heritable genetic basis for such trait differences. Since exploring existing LTER data or samples alone is not sufficient for addressing the core research questions, we will also use the workshop to develop new hypotheses and inspire a new research agenda centered around the selection of few, collaborative study systems in which to ideally test these plastic and evolutionary principles.

5.1 CAP LTER datasets

We have identified four kinds of long-term datasets collected by CAP that can contribute to either immediate analysis or defining hypotheses for future research. These datasets vary in their "off the shelf" readiness for use in the workshop. Our workshop proposal includes funding for a graduate research assistant (RA) who will work with the PIs and CAP LTER data managers to compile information about these datasets in a format accessible to the participants.

1) Samples - CAP retains collections of all arthropod and soil samples as well as some plant material from a fertilization experiment (Allen et al. 2018; McIntyre 2018). In addition, there are other repositories of samples in the Phoenix area, access to which could be coordinated through CAP partnerships (e.g. ASU Natural History Museum, NEON Respository, Desert Botanical Garden). These collections present an opportunity to take direct trait measurements and to extract DNA for time-series analyses. However, the condition of these samples has not been examined, and the data catalogs need to be summarized in a way that researchers can assess the viability of their use for these analyses. A graduate RA will carry out this work under guidance of the PIs and CAP LTER's data manager in preparation for the workshop.

2) Trait data sets - Some CAP scientists have already collected long-term trait datasets (>10 years) on their focal study organisms, which may be very useful to assess directions and causes of phenotypic change over time. These include long-term data on expression of sexually selected plumage coloration (in a well-studied songbird, the house finch, *Haemorhous mexicanus*) across the urban gradient (Giraudeau et al. 2018). Monitoring shifts in plumage can assess temporal and spatial change in this condition-dependent sexually selected trait (i.e. linked to male survival and to reproductive success). Additionally, lizard data (species, mass, length, unique ID number) from trap arrays on the Phoenix-Mesa Gateway Airport may highlight adaptations to urban substrates and shifts in traits over time (Battles et al. 2018). The spatial extent of these CAP datasets is often limited (i.e. to a few representative sites), but they represent an untapped resource for initial trait-based studies of urban evolution. The graduate RA will assist PIs with exploratory analyses of these trait data and the viability of these systems for potential long-term collaborative investments (i.e. see new research agenda above in sections 1 and 4).

3) Population and community datasets - Developing a synthetic understanding of eco-evo-plasticity dynamics requires basic data on the distribution and abundance of species, their associations

with key human resources selective agents, and changes over time. CAP LTER has over two decades of count data for birds and arthropods, collected across a range of land-use and land-cover types and across the entire metropolitan region. Data on herpetofauna and mammals are also available over a shorter time series. Several analyses of temporal trends have been published (Banville et al. 2017; Allen et al. 2019; Warren et al. 2019), along with ongoing assessments of how food and water resources may be linked to avian population trends (Brown et al. in prep., Grade et al. in prep.). These biological datasets are taxon-scrubbed, well-curated, and ready for use in the workshop.

4) Environmental datasets - CAP either directly collects or processes and curates existing datasets on land-use and land-cover, sociodemographic data, temperature, rainfall, noise levels, and soil properties from across the Phoenix metropolitan region. In addition, the Phoenix Area Social Survey (PASS) captures long-term changes in human perceptions of the environment, including specific questions on human-wildlife interactions. These data are essential for characterizing drivers, feedbacks, and spatio-temporal context of the heterogeneous social-ecosystems in which eco-evolutionary-plasticity dynamics occur. This makes CAP LTER a particularly ripe site location, not just for integrating evolutionary biology into the LTER program, but also for facilitating new interdisciplinary perspectives.

5) Social datasets - The PASS captures long-term changes in human perception of the environment and environmental attitudes. These perceptions and attitudes can be paired with environmental data and species population data to understand potential human-wildlife interactions and how these may drive reciprocal feedback loops between humans and the environment (e.g. Andrade et al. in review). Further, there is an increased effort in capturing attitudes towards specific taxa in the PASS 2021, and these attitudes can be extrapolated to link perceptions of traits across taxa. Two additional social data sets also exist and further address attitudes toward snakes as well as perceptions of what wildlife belong in cities.

5.2 Socio-eco-evolutionary-plasticity (SEEP) integration

While it is widely accepted that human social processes are a primary driving force behind altered eco-evolutionary dynamics in urban ecosystems, urban evolutionary ecologists have typically captured these processes in relatively simple terms, such as "human activity" (Alberti et al. 2017) or urbanization gradients (Johnson & Munshi-South 2017). In outlining a 'roadmap for urban evolutionary ecology,' Rivkin et al. (2019) highlighted the importance of understanding how the heterogeneity within cities influences evolution, acknowledging that "Cities are a mosaic of habitats that change through time, and over small spatial scales." These mosaics are shaped by multi-scalar human processes: individual- or household-level decisions shape yard management; collective social dynamics like enforcement of social norms can influence neighborhood characteristics; institutional processes like zoning policies impact city-wide or municipal scales and can have long temporal legacies (Andrade et al. 2021; Des Roches et al. 2021). Co-PI Schell and colleagues (2020) recently demonstrated how systemic racism shapes the distribution of vegetation cover and built structure both through legacies of institutional processes like redlining and ongoing power structures. These calls highlight the need for greater integration of social science in eco-evolutionary scholarship to more fully understand the spatio-temporal structure of selective forces operating on urban animal populations, as well as their implications for human well-being. CAP LTER scientists have been among the leaders in developing increasingly complex models of social-ecological processes (Childers et al. 2015; Grimm et al. 2017; Groffman et al. 2017; Pickett et al. 2017; Andrade et al. 2021), yet these models rarely grapple with evolutionary processes. When they do, they gloss over the details of organismal components (behavior, morphology, physiology) that are the mechanistic building blocks, frequently defining how animals do or do not respond to urban selective forces. Thus, the workshop provides an important opportunity for bringing together leaders in these two interdisciplinary arenas - eco-evolutionary dynamics and social-ecological systems - to address the key unanswered questions at this socio-eco-evolutionary-plasticity nexus.

6. Workshop Topics and Logistics

Tempe, Arizona is the home of Arizona State University (ASU) and also sits centrally within the Phoenix Metropolitan area, with easy access to airlines and light rail to gather participants from both within the region and beyond. ASU has the requisite conference room and video conferencing capacity (see Facilities document). We target February 2022 for holding the workshop, which provides us time during summer, fall, and winter 2021 to organize the meeting and gather the necessary information on available samples and datasets to make the workshop productive. We also hope that, by February 2022, larger in-person gatherings should be possible again.

The workshop will be organized around 5 thematic sessions, with cross-cutting and integrative discussions held at the end of each day. Each of our 5 urban resources and selective agents (heat, food, water, pollution, and species interactions) will comprise its own session. These themes provide a focal point for examining the complex interplay of social, ecological, evolutionary, and plasticity processes in cities. In addition, each of these topics are of major importance to human health and well-being. An explicit emphasis will be placed in each session on examining social processes through the lens of environmental justice (Schell et al. 2020; Miriti et al. 2021). For example, each session will address how historical and contemporary inequitable policies contribute to the spatiotemporal heterogeneity of each selective agent, enabling us to pinpoint the convergence of ecosystem disservices, environmental inequity, and biodiversity loss.

Each thematic session will begin with a set of research presentations (3-hour morning block) followed by a working session (3-hour afternoon block) structured around a common set of prompts:

- To what extent can we leverage existing LTER samples and datasets to address components of the central question? In other words, what analyses could we do with what we already have?
- What new research, building on LTER data, is needed to distinguish among different evolutionary mechanisms? What experiments? What comparative work across taxonomic groups is needed to quantify the prevalence of different social and ecological mechanisms?
- How can CAP and other LTER sites build organismic long-term data collection into their core monitoring? And in which model study organisms?

Partially hybrid workshop model – In-person interactions are essential, we argue, to making concrete progress on the workshop goals. However, we will use a hybrid in-person/virtual model for the presentation component of the workshop in order to facilitate broad participation of those not local or travelling to the area. The presentations in each session will be live-streamed, and virtual participants will be able to join digital workspaces to share thoughts and ideas triggered by the presentations.

7. Recruitment of presenters and other participants

The panel of 20-25 speakers (i.e. 4-5 speakers in each of our 5 sessions) will be selected based on their expertise either (a) within the session theme or (b) in relevant cross-cutting themes, then invited by the organizing committee. Criteria for speaker selection will be broad, examining factors other than typical metrics like the number or impact factor of the potential speaker's publications, or their profile as invited speakers in previous conferences. These metrics have well-known biases toward scholars who are white and male (Eaton et al. 2020; Maas et al. 2020; Schell et al. 2020). Rather, we will solicit participation through social media (e.g. #BlackBirdersWeek, #BlackMammalogists, #BlackBotanistsWeek, @BlackInX, @BlackAFinSTEM, @500QueerSci) and networks that support scholars from marginalized groups (e.g., the Black Ecologists Section of the Ecological Society of America, DiversifyEEB, The Wildlife Society Inclusion, Diversity, Equity, and Awareness Working Group). In addition, Co-PI Schell is the Diversity Officer Chair for the Animal Behavior Society and will use his networks to recruit participants. All organizing committee members will be responsible for making active contact with potential speakers and participants by phone and email. We acknowledge that our efforts to achieve comprehensive diversity - across race, ethnicities, gender, sexual orientation, ability, income, etc. - will be incomplete and not representative of the US population. However, through

the implementation of these relatively non-traditional practices, we aim to significantly improve the diversity of participants and speakers of this meeting relative to past meetings.

Within each session, speakers will represent a diversity of disciplinary perspectives within our SEEP framework - Social, Ecological, Evolutionary and Plasticity (e.g. behavior, morphology, physiology). Each session will also include a mix of CAP LTER affiliated scholars and non-CAP scholars; we plan to invite at least 2 non-CAP scholars per session (2 x 5 sessions = at least 10 outside speakers total). We will target the inclusion of BIPOC and early-career scholars (both CAP and non-CAP) as speakers for all sessions. We will pair a CAP scientist with a non-CAP scholar as co-leaders for each session (see Section 2 above). Details of session planning will be adjusted based on feedback from the participants through a pre-workshop planning process (see Section 10 below for full timetable).

Child and Family Care Options - To further maximize inclusivity, we have allocated funds in the budget to provide financial support for childcare, both to those who are travelling and those who are remotely participating and still needing at-home support. For travellers, such funds could be used to cover the additional costs for a caregiver to travel with the participant to Arizona or to hire a licensed child-care provider on site. This information will be included in the recruitment messages to potential participants about the workshop.

8. Agenda and Session Descriptions

Introductory session - SEEP Framework

The short opening session will include an introduction to the CAP-LTER program (Dan Childers - ASU, CAP leader), an overview of the field of urban evolutionary ecology by Chris Schell (University of California-Berkeley, newly joined CAP member), and a presentation of key driving questions in urban evolutionary ecology by Sarah Diamond (Case Western Reserve U, non-CAP). In addition, the graduate RA will provide an overview of the datasets and sample collections at CAP that were compiled during the pre-workshop planning phase.

Opening speakers and moderators will also advance fundamental eco-evo questions that motivate the workshop, such as: Does plasticity forestall or facilitate evolution in cities? Are there traits that predict when plasticity or evolution will be more important for coping with city life? How does selection, as the mechanism of adaptive evolution, interact with non-adaptive processes (drift, mutation, migration)? What are the ecological and social consequences of evolutionary and plastic responses to urbanization?
Moderators: Kevin McGraw (CAP LTER), Ryan Martin (Case Western Reserve Univ.; senior personnel)

Theme 1 - Heat

As one of the hottest cities in the United States, Phoenix is an ideal site for examination of the evolutionary implications of the well-known urban heat island (UHI) effect (Brazel et al. 2007). CAP scientists have documented a myriad of social, ecological, and physiological effects of the UHI, as well as its spatiotemporal heterogeneity. Diamond and Martin (2020) have recently reviewed the literature on how the UHI shapes urban evolutionary biology. Most notably, while they note a handful of studies providing evidence for morphological, physiological, and life-history shifts in urban organisms, the take-home message from their review is two-fold. First, taxonomic coverage is quite limited. Second, few studies provide the common garden or transplant experiments that allow us to disentangle evolutionary responses from phenotypic plasticity. Our workshop will address these two concerns head on—working to find study systems and long-term datasets that allow us to increase the diversity of urban organisms studied and to move towards more complete studies that tackle plastic and evolutionary mechanisms.
Moderators: Chad Johnson (CAP LTER) and Kristien Brans (Belgium; tentative external)

Theme 2 - Water

As an LTER based in the urban desert of Phoenix, Arizona, CAP has been an undisputed leader in studies of the role of water for both the urban ecosystem (Sampson et al. 2020), and the feedback to the human population and their health (Wutich et al. 2020). Water inputs from humans can create oasis-like effects in a desert city, decoupling populations fluctuations in arthropods from precipitation and even forming novel riparian habitats. At the same time, organisms may be water-stressed in areas with high levels of pavement or heat exposure. We know relatively little about how water acts as a unique urban selection pressure on the populations of organisms that are evolving in our cities. Water limitation in the desert could interact with the UHI to affect critical traits such as thermal tolerance levels and behavioral shifts in foraging or site preferences. This session will highlight the strengths of CAP's water datasets, and allow us to coalesce around a new urban evolutionary ecology of water.

Moderators: Fuschia-Ann Hover (CAP LTER), Simone Des Roches (Univ. Wash.; tentative external)

Theme 3 - Pollution

Pollution in urban environments is multifarious, ranging from heavy metals, environmental toxins, and pharmaceuticals in soil and water, to sound, light and particulate pollution of the air. These are often potent agents of selection (Isaksson & Bonier 2020). Broadly, pollutants can lead to maladaptive behavior, reduced immune defenses, and negatively affect fecundity and survival. Importantly, many organisms are able to compensate for these effects via rapid, adaptive evolutionary responses and phenotypic plasticity. For example, chemical pollutants in water runoff have led to entire restructuring of pace-of-life syndromes in urban water fleas (Brans et al. 2018), great tits have evolved greater tolerance of heavy metals (Perrier et al. 2018), moths have evolved decreased sensitivity to light pollution (Altermatt & Ebert 2016), and urban frogs and birds plasticically modify their vocalizations in response to city noise (Sepp et al. 2020). Although progress has been made to quantify these plastic and evolutionary responses to the diverse suite of pollutants in cities, few studies contend with the fact that these agents of selection are not distributed evenly across the landscape, covarying with socioeconomic and racial compositions of neighborhoods (Schell et al. 2020), carrying mutual implications for the health of humans and non-humans alike. How multiple agents shape evolutionary trajectories of populations, particularly in the context of spatio-temporal heterogeneity in cities, is an important frontier that could be advanced with LTER datasets.

Moderators: Ryan Martin (Case Western Reserve), Jessica Hua (SUNY Binghamton; tentative external)

Theme 4 - Food

Organisms in urban environments often experience changes in food quantity and quality, including introduction of human-provided subsidies, shifts in main nutritional/prey base, and associated alterations in energy use and movement/foraging ecology. Food subsidies are also spatially and temporally heterogeneous across urban landscapes in ways that may or may not align with human food deserts, and the ways that animals alter their populations, behavior, and morphology in response to food have direct implications for human-wildlife interactions. CAP scholars have drawn attention to the cascading ecological effects of food subsidies through populations and communities (Shochat et al. 2004; Faeth et al. 2005). Standardly lacking in this urban nutritional-ecology literature, however, is a firm understanding of evolutionary causes and consequences at the organismal level – i.e. what variation predisposes organisms to adjust nutritionally in urban settings, and what are the fitness consequences of such anthropogenic food alterations? In this session, we aim to address these questions by building on feeding-ecology expertise from the CAP community and engaging with evolutionary physiologists and evolutionary ecologists. We will emphasize employing genotypic/phenotypic trait-based approaches to better understand how the altered food resource uses of urban animals contribute to socio-eco-evo-plasticity dynamics.

Moderators: Kevin McGraw (CAP LTER), Anne Charmantier (CNRS, France; tentative external)

Theme 5 - Species Interactions

As urbanization alters resources and habitat structure, community composition and function are being fundamentally altered (Swan et al. 2011; Aronson et al. 2016). For instance, the relative abundance and distribution of native to non-native species are driving novel species interactions that can either facilitate or impede local adaptive processes (Lambert & Donihue 2020). In certain instances, other selective agents (e.g., food subsidies) can coincide with community dynamics by influencing the movement patterns of certain urban wildlife, bringing them into conflict with humans or other urban species (Rodewald et al. 2011; Newsome et al. 2015; Lamb et al. 2017; Penteriani et al. 2018). Competition for limited resources between urban fauna may result in local extinction of the less-tenacious species, which often means the loss of native or endemic wildlife (Shochat et al. 2010; Faeth et al. 2011). Rapid changes to the urban landscape via habitat loss or transformation can restrict habitat connectivity for essential pollinators (Jha & Kremen 2013; Lopez-Uribe et al. 2015) or in some instances positively affect insect pollinator abundance and diversity (Hall et al. 2017). Further, direct interactions between humans and wildlife can serve as a selective filter, in which certain species are permitted or excluded due to the prevailing cultural and individual values of those species across urban neighborhoods (Aronson et al. 2016; Schell et al. 2020). However, to date few investigations have enumerated whether such novel species interactions facilitate or impede evolutionary responses of organisms to urban living. Recent studies suggest that certain aspects of built environments may serve as ecological traps (Russo & Ancillotto 2015; Lamb et al. 2017), with others demonstrating that community interactions are mediated by de facto human shields (Moll et al. 2018; Gallo et al. 2019; Parsons et al. 2019), but evidence of changes in allele frequencies due to these interactions are scant. Here, we will emphasize how community-level interactions, and the varied results from those interactions, could drive or inhibit urban evolution.

Moderators: Chris Schell (CAP LTER), Nyeema Harris (University of Michigan; tentative external)

Synthesis and Work Sessions

The last session of each day will be devoted to identifying cross-cutting research questions, analyses, or project ideas that touch on main workshop themes. We will use digital workspaces like Padlet, MURAL, or Jamboard for capturing ideas throughout the presentation sessions. McGraw and Warren effectively used Padlet at the previous CAP LTER workshop. These workspaces and notes from day 1 can also be reviewed by the session leaders to extract ideas with which to seed day 2 work sessions. We will devote an additional half-day after the presentation sessions to begin development of the workshop products.

Moderators: Paige Warren (CAP LTER), Sarah Diamond (Case Western Reserve University)

9. Expected Products and Dissemination

We anticipate that our workshop will yield four major products: (1) a core aim is to construct a **long-term research agenda for evolutionarily-themed LTER work**, permitting a focus on one/few model study systems in which to investigate central genetic, epigenetic, behavioral, and environmental themes in urban evolutionary biology; (2) Participants will co-write at least **one large synthesis paper** (e.g. literature review, meta-analysis), tying in key, new concepts and approaches from the evolution-/plasticity-focused workshop, and with emphasis placed both on the categories of human resources and selective agents that motivate the workshop as well as the applicable study systems of our workshop researchers. A similar, smaller-scale product emerged out of our group's pilot workshop on urban heat, food, and water in January 2020; (3) Participants will also write a **white-paper** report **on LTER data collection procedures**, to equip other LTER sites and researchers with the tools and methods for conducting and better supporting evolutionary biology research within the network; (4) **A presentation** of this workshop's themes and outcomes will be delivered by workshop leadership **at the annual LTER**

network's all-scientists meeting in Fall 2022, with the goal of broadening our reach to other network partners and recruiting additional collaborators and research systems into this initiative.

10. Timeline for Workshop Preparation and Product Development

- *August 2021* - The organizing committee will meet to finalize the list of co-leaders for the themed sessions and map out plans for the meeting website.
- *September 2021* - The graduate RA will work with the organizing committee and the ASU Communications teams to finalize the website and announcement of the workshop.
- *Fall semester 2021* - The graduate RA will work with Stevan Earl (CAP information manager) and Quincy Stewart (CAP site manager) to gather information on available data and samples in advance of the workshop.
- *October 2021* - A virtual meeting with session co-leaders will review gathered materials and revise plans for the workshop. A call for speakers and participants will be generated from these discussions.
- *November 2021* - Registration and abstracts will be due for the workshop.
- *December 2021* - The organizers will complete processing of registrations, abstracts, and scheduling by the end of the year. In addition, the graduate RA will work with the organizing committee to finalize the list of priorities and preliminary analyses with long-term CAP data/samples.
- CAP All Scientists' Meeting, January 2022 - We will publicize the workshop at the annual CAP symposium. The organizing committee will meet to finalize the workshop plan and send guidance to participants on their presentations.
- *February 2022* - workshop is held on the ASU-Tempe campus
- *March-May 2022* - The graduate RA will assist the organizers with follow-up work, including analyses of biological samples or other CAP datasets. Symposium leadership will also work with respective participants on the white paper and other synthesis products.
- *Summer 2022* - target date for completion of white paper and other synthesis products

11. Broader Impacts

We focus on three forms of broad impact in our workshop: *training, science communication, and community engagement*. Taking an explicitly JEDI-centered approach in all aspects of the workshop - from recruitment and advertisement through session participation and topics - will be pivotal to ensure that we proceed inclusively in this field of urban evolutionary biology.

Training: The workshop will provide an opportunity to train early-career scholars and integrate them into a larger working group on urban evolutionary biology. Early in workshop planning, we will conduct broad searches for underrepresented groups in this field, including early-career Black and Indigenous persons of Color (BIPOC) scholars, in order to ensure that their perspectives on the legacies of urban racism are represented and amplified in development of our SEEP framework. Workshop funding for these traveling participants will be key to reducing barriers to entry and participation in the field. We also anticipate integrating into our workshop justice, diversity, equity, and inclusion (JEDI) training, to decenter whiteness in our academic spaces and improve understandings of inherent biases within STEM disciplines, urban evolutionary ecology included. Further, the workshop will act as a conduit for collaborations within the CAP LTER network, serving to connect a broad and academically diverse group of both ecological and social scientists. These emerging professional networks will result in impacts that extend beyond the workshop by seeding future LTER collaborations. As many of the workshop leaders are senior personnel in their field, early-career scholars will have the benefit of learning and working directly with these researchers.

Science communication: To further promote interests in urban nature both locally and nationally, we will also curate and produce a podcast series titled "SEEP This!" that emerges from the workshop content and outcomes. This 5-episode limited series will be mapped directly onto our workshop themes

(i.e., heat, water, food, pollution, species interactions), with our leadership team and additional workshop contributors as experts on the selected themes. Moreover, the language, examples, and case studies will be made accessible for audiences in K-12, undergraduate, academic, and lay audiences interested in wildlife, nature, evolution, and conservation in cities worldwide. Co-PI Schell has previously contributed to a similar podcast series for a Pacific Northwest-based podcast series called EnviroAmplify, which centered on the environmental experiences of Tacomans and the general Pierce County region (https://earthlab.uw.edu/grants/2019-2020-funded-projects/voices-unbound/). Through the support of the Strategic Marketing and Communications team within ASU's Knowledge Enterprise (led by Jason Franz), the promotion and outcomes of this next workshop will be amplified through the appropriately identified channels and assets within the Julie Ann Wrigley Global Futures Laboratory portfolio of social-media channels and newsletter distribution lists. These channels span internal audiences as well as have other local, regional and global reach. To additional foster outside media interest in our workshop and podcasts, our leadership team will engage with ASU's media-relations team to extend pitches to a variety of targeted media outlets (e.g. NY Times, Wall Street Journal).

Community engagement via Ecology Explorers: Finally, we will work closely with the Ecology Explorers program established in the CAP LTER program at ASU to connect K-12 and undergraduate students with scientific research experiences that are integral to the success of the larger CAP LTER mission. Students will be involved in workshop-derived data collection and synthesis activities that (a) work to describe how urban heat islands affect human and non-human organisms; (b) explore how water sources are distributed across the local landscape via geographic and landscape-ecology techniques; (c) learn about long-term datasets and analysis; and (d) build effective science communication skills to disseminate research findings to the broader community outside academia. These myriad facets of community engagement will provide a platform that demystifies the process of ecological and evolutionary research, while providing a direct interface with local community members on environmental issues pertinent to the region. The workshop leadership team has connected with Monique Franco, CAP LTER Outreach and Education Coordinator, who will partner with us as part of the workshop to identify candidate local schools, teachers, and community organizations for these efforts and ensure we create curriculum- and standards-aligned educational resources.

12. Results from prior NSF support

Diamond (PI): *CAREER: Butterflies on the move: integrating biogeography, physiology and citizen science towards a mechanistic understanding of contemporary climate-driven range shifts* (DEB-1845126). 2019-2024. $724,926. Intellectual Merit: Improves forecasts of climate-driven range shifts via incorporation of physiological trait variation and mechanism. Publications: Diamond & Martin 2020, 2021, in press; Chick et al. 2021; Lambert et al. 2021. Broader Impacts: Trained 1 post-doc, 2 graduate students, 3 undergraduates (all women, 2 from underrepresented groups); 2 international conference presentations, and 2 institutional presentations; created educational modules for K-5 students to learn about butterfly life cycles and impacts from environmental change.

McGraw and Warren (co-PIs): *Central Arizona–Phoenix Long-Term Ecological Research IV* (DEB-1832016), 2018-2022. $4.5 million. Intellectual Merit: Advancing knowledge about the interconnectedness of human motivations, behaviors, actions, and outcomes with urban ecosystem structure and function. Broader Impacts: Trained 10 graduate students, 4 undergraduates, 1 post-doc; created lesson plans and internships through the K-12 Ecology Explorers. >37 conference presentations. Publications: Giraudeau et al. 2018; Hutton et al. 2018; Weaver et al. 2018; Allen et al. 2019; Hensley et al. 2019; Warren et al. 2019; Weaver et al. 2019; Brown et al. 2020; McGraw et al. 2020; Andrade et al. 2021, in review; Arnold et al. 2021; Hutton et al. 2021; Mills & McGraw 2021; Sykes et al. 2021; Schaper et al. in press.

Warren (co-PI) *Collaborative: RCN: UrBioNet: A Global Network of Urban Biodiversity Research and Practice*. (DEB-1355151; Population and Community Ecology Cluster; 2014-20; $282,930). Intellectual Merit: Gathers global databases, provides planning tools, and conducts research to

advance knowledge, aid in species conservation, and offer new insights into urban planning in an urbanizing world. Publications: Aronson et al. 2014, 2016, 2017; LaSorte et al. 2014, 2018; Dolan et al. 2017; Lepczyk et al. 2017a,b; Nilon et al. 2017; Hensley et al. 2019; Kuras et al. 2020. Broader Impacts: UrBioNet (>350 members, 30% students) engages scientists and managers globally through workshops. Training: 2 postdoctoral researchers, 12 graduate students, 12 undergraduates, and 160 professionals.