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The respect it deserves: Book review of Szulkin, M. , J. Munshi-South, and A. Charmantier, eds. 2020. Urban Evolutionary Biology. Oxford University Press, Oxford, 303 pp. ISBN 978-0-19-883685-8; $ 49.95 PB

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As a graduate student in the late 1980s and early 1990s I was struck by an undercurrent of discrimination against behavioral biologists who studied domesticated, zoo, or urban animals, and ecologists who studied species around people. Cities?! They are not "natural." Field biologists, after all, should go to "natural" places and study "natural" processes. But what is natural? Naturalness is, of course, not absolute. An older definition I like is that it reflects the amount of human energy that has gone to modify the system (Anderson 1991); a site with paved roads and buildings is less natural than a site with dirt roads and cabins. But this definition reflects intentional modifications and doesn't recognize our planetary chemical footprint that includes Persistent Organic Pollutants (Roscales et al. 2016) and plastics (Geyer et al. 2017) to name a few. Restricting our studies to "relatively" natural areas is limiting. How are we to understand and manage biodiversity around ecotourism or our expanding urban footprint? And, the irony was that studying *Drosophila* and *Tribolium* in jars and *Daphnia* in mesocosms was somehow OK because they were "model systems." I will be the first to admit that we have learned a lot from model systems and I am delighted to see that we have realized that we have a lot to learn from cities! Now, we not only recognize that studying the behavior, ecology, and evolution of urban species provides unique opportunities to study foundational processes, but it also is essential if we are to wisely manage biodiversity and increase urban sustainability on an increasingly urban Earth.

Humans have a long history of habitat modification and there have been two major human-driven transitions, as Milot and Stearns nicely remind us in the final chapter of *Urban Evolutionary Biology*. First, there was a transition to agriculture, which created a series of novel anthropogenic environments. Only later was there a transition to larger population settlements. Now, over 50% of humans live in cities (United Nations 2018) and cities occupy 3% of the Earth's habitable land (Center for International Earth Science Information Network – Columbia University et al. 2011). The proportion of people in cities, and cities themselves, are expected to grow substantially in the coming decades (Seto et al. 2012). These transitions have clearly influenced the distribution and abundance of organisms on Earth and because of their impact, urban areas may provide replicated experiments, much like islands, to study ecological and evolutionary processes that occur in cities and indeed provide a novel model system for studying adaptation.

Urban Evolutionary Biology is a wonderful compilation of the diversity of ways that urbanization can influence evolution and evolutionary processes. *Urban Evolutionary Biology* is part tutorial, part review, and part preview that will set the course of the study of evolution in urban areas for decades. It is must reading for graduate students who want to make an impact—whether it is a scholarly impact or an applied impact. In 16 chapters it covers evolutionary principles in cities to specific phenomena (sidewalk plants) and ends with a fascinating chapter on human evolution in cities.

Chapter 1 is an overview by the editors who are commended to bring together an international and diverse set of scholars to contribute to this book.

In Chapter 2, Szulkin et al. tackle the difficult question of how does one quantify urbanization. They note that "…it is the ultimate replacement of all natural elements…by man-made ones…" (p. 14). Yet, even this is not straightforward and requires assumptions about development, space, and time. Importantly, different species may respond differently to the same features in the build environment. These are not insurmountable challenges but they must be considered. They also note that it is not possible to separate the biological variables from the human cultures and preferences that are associated with urban areas. This theme highlights the essential role of massively interdisciplinary scholarship if we are to develop robust theories of urban evolution and manage cities based on scientific insights (I expand on this at the end of this review). They include a very useful supplement that contains resources to quantify urbanization and human impacts.

Want to have fun while locked down? I suggest a parlor game. Gather some friends—through Zoom of course in these times of global pandemic—and instruct everyone to write a scholarly paragraph that describes how the world is urbanizing and what the consequences are for evolution and biodiversity. It turns out there are a few key references (I've cited some above) that will be in them all and what you will see might resemble the convergence seen in the opening paragraphs of a number of chapters in this book. Parallelism at its best! Which brings us to Chapter 3 where Santangelo et al. remind us of the obvious fact; there are a lot of cities and this gives us the opportunity to use them as replicates. Replication can be used to understand if there are similar evolutionary responses in different cities—parallelism—that may shed light on the possible pathways of adaptation. Several things may lead to variable responses. For instance, increased genetic complexity should lead to less parallelism, and spatial heterogeneity in cities will increase variation. Importantly, spatial heterogeneity will affect species differently and they note that parallelism may vary among traits. Variation among traits in evolutionary responses to urbanization is a theme that reoccurs throughout the book.

In Chapter 4, Munshi-South and Richardson focus on landscape genetic approaches to understand movement and gene flow in cities. The matrix of buildings, green space, utilities, and roads, as they note, is structured in ways that we often do not see in nature. The chapter is a great introduction to some of the methods and questions in studies of landscape genetics.

In Chapter 5, Perrier et al. focus on adaptation genomics. The challenge of all studies of adaptation in urban areas is that we see many phenotypic differences in many traits, but it's quite difficult to determine whether these reflect plasticity (Hendry et al. 2008) or actual genetic adaptations (Pelletier and Coltman 2018). The authors nicely review quantitative and population genetic methods to study this and have an interesting section on epigenetics in urban areas.

When we think of what is different in urban areas compared to natural areas, two things immediately come to my mind—the built environment (i.e., the roads, buildings, and utility infrastructure that we have built) and urban heat island effects (cities are hotter than adjacent rural areas). In Chapter 6, Diamond and Martin describe what is known and known about the evolutionary consequences of the urban heat island effect. Here too the main challenge is teasing apart plasticity versus evolutionary responses. Reciprocal transplants and common garden experiments have been useful tools to study this, but of course, these are restricted to a subset of species amenable to such manipulations. They reviewed published studies and found that urban heat islands had varied effects on different traits, and from this they called for more publication of null results so that the true effect of urban heat islands can be understood in the future.

Edited volumes like this offer authors the ability to preview a literature and guide future discovery. In Chapter 7, Irwin et al. wonderfully preview a literature on how cities influence mutualisms. Mutualisms, they remind us, are quite sensitive to context and urban areas change the costs and benefits of cooperation. Changes may break down a mutualism or even drive it to become a parasitic relationship. There are dissertation projects waiting to be conducted by careful readers of this chapter.

In Chapter 8, Chaptou and Lambrecht note that sidewalk plants are a unique system in cities. They remind us that cities create novel problems and challenges for organisms. In the case of plants, they often create unique geometries (isolated patches surrounded by concrete matrix) that can be viewed as replicated experimental units that are ripe for study because individuals living in cities may systematically differ from those living in more natural rural areas.

In Chapter 9, Gorton et al. review evidence of adaptive evolution of plant life histories in urban environments. Highlighting methods (including reciprocal transplants), and noting that there may be both counter-gradient variation and co-gradient variation,

they wisely point out that not all differences may be adaptive and chart a path for future studies.

In Chapter 10, Langerhans and Kern note that more is known about the ecological effects of urbanization on aquatic organisms than evolutionary effects. This chapter is thus mostly a structured preview of future studies. However, rapid evolutionary responses to some pollutants, as well as thermal and hydrological shifts, have been reported in some species. Here too, the authors recognize that not all species and not all traits respond similarly to urbanization which creates both challenges and opportunities for future studies.

Chapter 11, by Brans et al. continues the theme of previewing the future in their chapter on evolutionary dynamics of metacommunities. We expect metacommunities to evolve and we need to understand key feedback loops that drive evolution. Dissertations will emerge from a careful reading.

Most animals have to move around, and urbanization modifies the substrate on which they move. In Chapter 12, Winchell et al. focus on evolutionary responses in terrestrial locomotion. After noting the relative paucity of studies, they go on to preview what can be studied and boldly predict anticipated results.

While a literature of the effects of pollutants on physiology exists, Isaksson and Bonier in Chapter 13 seek to focus and frame the future study of urban evolutionary physiology. They recognize the challenges in part because most urban factors are not inevitably toxic, but rather their effects depend on dose and there may be both beneficial and detrimental effects. Again, the chapter should pay dividends to careful readers.

Early studies of aquatic and sound pollution's impact on behaviors focused on what were likely sexually selected traits. A decline in water clarity associated with eutrophication impacts mate choice in fish (Seehausen et al. 1997), anthropogenic noise makes bird songs less sexy (Halfwerk et al. 2011), and more recent reviews have synthesized the effects of pollution on sexual selection (Candolin and Wong 2019). In Chapter 14, Sepp et al. review and propose other sexually selected systems that are (or could be) impacted by urbanization. It is difficult to predict how urbanization influences sexually selected traits because available evidence has its examples both strengthening and relaxing its force. The authors wisely break down the problem into how it might affect signalers and receivers. They conclude that many findings to date may reflect plastic responses to urban environments, but also note that a plastic response in one trait may create novel selection pressures on other traits.

Cognition, as Sol et al. tell us in Chapter 15, includes "…the neural processes that regulate how animals gather, preserve, and use information…[which permits] individuals to improve decision-making and problem solving when confronted with novel challenges" (pp. 254–255). Key stuff for responding to the built environment! Effective cognition, and particularly learning, may buffer individuals from selection, and thus may weaken (but perhaps not eliminate) selection. Studies have shown that ecological generalists often do better in a variety of environmental contexts, including novel urban ones. Most of these studies have focused on dietary generalists who may suddenly experience a variety of new foods in cities. The challenge to really understand cognition's impact on evolution is to study individuals (many studies do not keep track of individuals) and document intraspecific variation in cognitive abilities. To date, many cognitive studies have focused on documenting abilities but not fitness consequences, which will be essential to understand its evolutionary effects.

In the final chapter (16), Milot and Stearns summarize the evidence that cities have driven human evolution. I really liked the evolutionary medicine structure of this chapter that both summarized what traits we know have changed, and point out traits that should be better studied. They reported that educational status can interact with urban life to influence fertility. Indeed, we know that there are many socioeconomic drivers that influence human health, and this highlights what I think was missing from this wonderfully inspiring and educational volume. I will focus on two lacunae below.

First, and despite this being an entire book about the consequences of urbanization for evolutionary biology, the human dynamics at play within urban areas were, to my reading, underrepresented and underexplored. I longed for a few more chapters! What I find so exciting about studies of urban biodiversity is that you get to hang out with and learn from a group of scholars you might not normally interact with—anthropologists, architects, engineers, experts in environmental justice and public policy, sociologists, urban planners, etc. If we are to develop actionable insights and predictive models of evolution in cities, and if we are going to improve human welfare and biodiversity we are going to have to understand what tools these different fields bring to the table and we're going to have to understand the constraints they identify. For instance, red lining, as Schell et al. (2020) recently explained, has had a profound effect on biodiversity, ecoevolutionary processes, and human health and wealth in U.S. cities. Lasting improvement will only come through truly interdisciplinary collaborations.

Second, I believe that the editors lost an opportunity to encourage their contributors to think about what the insights for application are. I am as guilty as others in this respect having written a number of what I like to call "prospective reviews" or "previews" of a topic. And, it certainly pops up here and there in vague terms about maintaining genetic diversity and preventing population subdivision. But conservation science calls for actions at the level of on-the-ground managers as well as policy makers (Blumstein 2020). What is in it for them? How can each chapter provide these key stakeholders actionable information. In

some cases, it is a stretch, but the same way that many contributors systematically worked through implications of urbanization for the phenomena they wrote about, they could have stretched a bit more and thought about actionable (or potential actionable) advice. More generally, I think that teaching our trainees how to apply scientific knowledge requires new skills and books like this that should be widely read by them have an opportunity to model it.

But these are just two things that I longed for while reading this stimulating book. *Urban Evolutionary Biology* should be on the shelf (or hard drive) of those interested in rapid evolution, experimental studies of evolution, and of course the evolutionary impact of humans on biodiversity. It would be an excellent book to discuss in graduate seminars, and entering trainees interested in anthropogenic impacts on biodiversity would be well advised to read it particularly closely.

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