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Adaptation to urban environments

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Despite widespread evidence of urban evolution, the adaptive nature of these changes is often unclear. We review different phenotypic and molecular lines of evidence used for assessing urban adaptation, discussing the benefits and limitations of each approach, and rare examples of their integration. We then provide a synthesis of local adaptation to urban and rural environments. These data were drawn from phenotypic reciprocal transplant studies, the majority of which focus on insects and other arthropods. Broadly, we found support for local adaptation to urban and rural environments. However, there was asymmetry in the evidence for local adaptation depending on population of origin, with urban adaptation being less prevalent than rural adaptation, suggesting many urban populations are still adapting to urban environments. Further, the general patterns were underlain by considerable variation among study systems; we discuss how environmental heterogeneity and costs of adaptation might explain system-specific variation in urban-rural local adaptation. We then look to the future of urban adaptation research, considering the magnitude and direction of adaptation in context of different agents of selection including urban heat islands, chemical pollutants, and biotic interactions.

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An introduction to urban adaptation: what do we know and how do we know it?

The extent to which natural populations are well adapted to their environment remains a contentious topic in evolutionary biology, and in part reflects the ubiquity of spatio-temporal fluctuations in selection pressures that might keep populations from reaching or staying at a fitness peak [1]. Synthetic studies generally conclude that there is a higher incidence of adaptation than maladaptation in natural populations, suggesting populations are at least reasonably adapted to their environment [2]. Cities, as novel and dynamic environments, likely contribute to the displacement of previously adapted populations from their ancestral fitness optima [3]. Although there is much evidence now that populations can rapidly evolve within cities, the extent to which these changes are adaptive is less well characterized [4•,5•,6•].

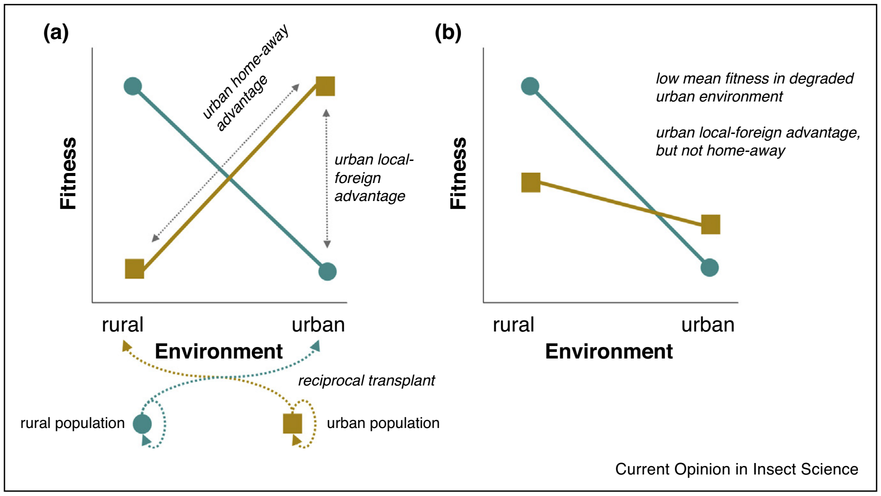
To do so requires demonstrating an evolutionary response to urbanization and demonstrating that these responses increase fitness within the urban environment. Reciprocal transplant experiments showing a fitness advantage to the urban population, either relative to the rural population within the urban environment, or within its home urban environment relative to the rural environment (Figure 1) provide the most direct evidence of urban adaptation [7]. Though, inferences can also be drawn from other phenotypic [8••] and molecular methods [9]. Here we review the current literature on urban adaptation to address two questions: (1) what are the benefits and limitations associated with different phenotypic and molecular approaches to understand urban adaptation? And (2) what is the evidence to date, gathered from reciprocal transplant experiments, that urban populations are adapting to urban environments, and how does this compare to the evidence for adaptation of ancestral populations in non-urbanized environments? Throughout, we highlight the many studies on these topics that come from insect systems [4•]. The relatively high proportion of urban (local) adaptation studies from insects is perhaps unsurprising given their ubiquity across rural-to-urban clines, their amenability to manipulation and transplantation, and their critical roles in ecosystem function [10].

Phenotypic and molecular approaches

There are two main starting points for assessing adaptive evolution, whether in an urban context or otherwise. Inferences can first be made at higher-order levels of biological organization that involve whole-organism phenotypes and their genetic underpinnings (e.g. heritability). Likewise, investigation can begin with lower-order levels of biological organization that involve molecular responses. Both have been used to examine urban adaptation, and each approach has its own benefits and limitations.

The main advantage of phenotypic approaches is that the linkage between phenotypes and fitness is much more direct. They allow for reciprocal transplantation

Figure 1



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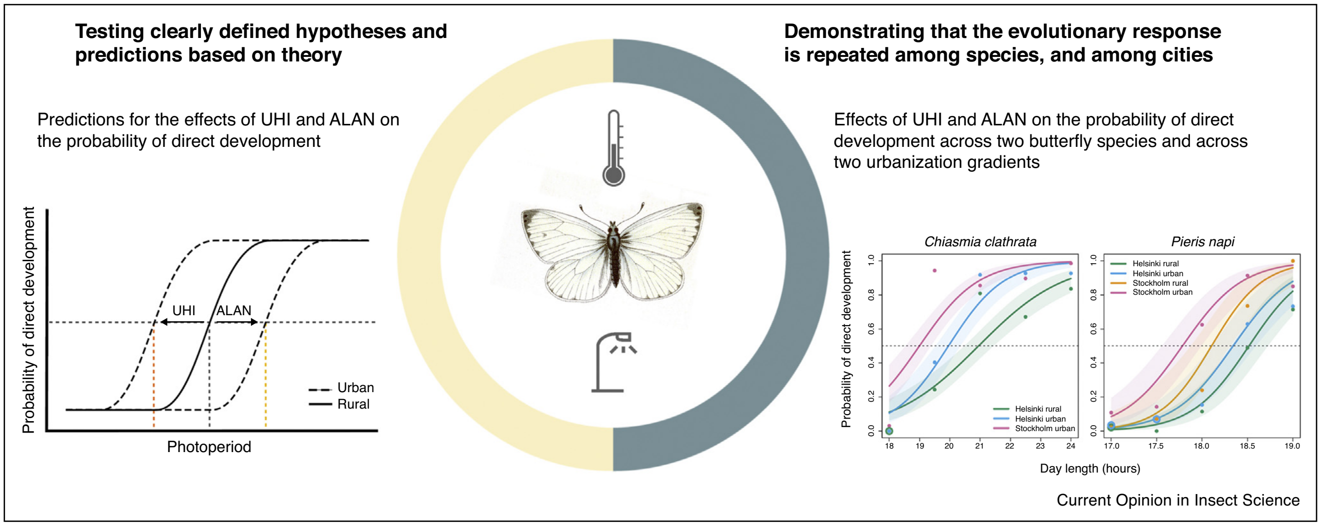
Testing local adaptation using reciprocal transplants. In this design, rural and urban populations are placed within ‘away’ environments and back into their ‘home’ environments (dashed curved lines with arrows, panel **(a)**, x-axis annotation). (a) Home-away and local-foreign comparisons can be used to test for local adaptation. Dashed straight lines with arrows indicate these comparisons from the perspective of urban population, though the same comparisons are possible from the perspective of the rural population (not shown, for simplicity). Fitness tradeoffs across environments are evident for urban and rural populations where each has maximal fitness in its own environment. **(b)** In degraded urban environments, maximal fitness might be reduced overall. In this example, urban populations have a local-foreign advantage, but not a home-away advantage, reinforcing the importance of local-foreign comparisons.

across urban and rural habitats and for the targets and causes of selection to be directly identified [4•]. However, it should be noted that approaches integrating phenotypic and molecular methods such as QTL mapping can be used within reciprocal transplant designs [11,12]. Assessing fitness responses of urban and rural populations in each others’ environments relative to their own and relative to one another within an environment provides a direct assessment of whether the populations are locally adapted (i.e. both local-foreign and home-away comparisons, Figure 1). Minor drawbacks of this approach involve measuring and interpreting fitness outcomes in the relevant environmental context. For example, in acorn ants, evidence of local adaptation to urbanization was first detected via fecundity in the lab [13]. However, in a subsequent field reciprocal transplant experiment, local adaptation was detected via survival whereas the results for fecundity were more complex. Surprisingly, rural ants had relatively high fecundity in urban environments, potentially owing to altered warm-season cues for reproduction in the field [14•], an element that was not present in the lab experiment. Yet, the main drawback with this approach is that there are constraints on the range of organisms for which reciprocal transplantation is an option. Large-bodied, high-dispersal ability organisms, or those for which containment is generally difficult, are unlikely or unethical candidates for reciprocal transplant studies [5•]. Despite this limitation, the breadth of organisms assessed via phenotypic approaches can be increased by taking other approaches beyond reciprocal transplants. Specifically, these include: (1) measuring the strength, shape and targets of natural selection [15,16]; (2) establishing links between morphology, performance and fitness [17]; (3) phenotypic manipulations that can directly assess function and its putative adaptive nature [18]; and (4) testing well-defined hypotheses from theory and combining these with replication among species and cities. As a recent example of this last approach, the repeated, predicted urban evolution of seasonal plasticity in development in response to urban heat islands across different Lepidopteran species and cities can be used to make a case for urban adaptation [8••] (Figure 2; interestingly, evolved shifts in developmental timing and growth were also seen in an urban damselfly, likely in response to extension of the growing season within urban heat islands [19]; finally, see also Ref. [20] for a multi-species, multi-city synthesis of studies showing the repeated evolution of higher heat tolerance in response to urban heat islands). With these approaches, common garden experiments are critical for showing whether the phenotypic divergence is due to evolved differences or phenotypic plasticity [21]. If phenotypic differences persist between urban and rural populations after being brought into a common (garden) environment, then this provides evidence of genetic, evolved differentiation. Including additional environmental

Figure 2



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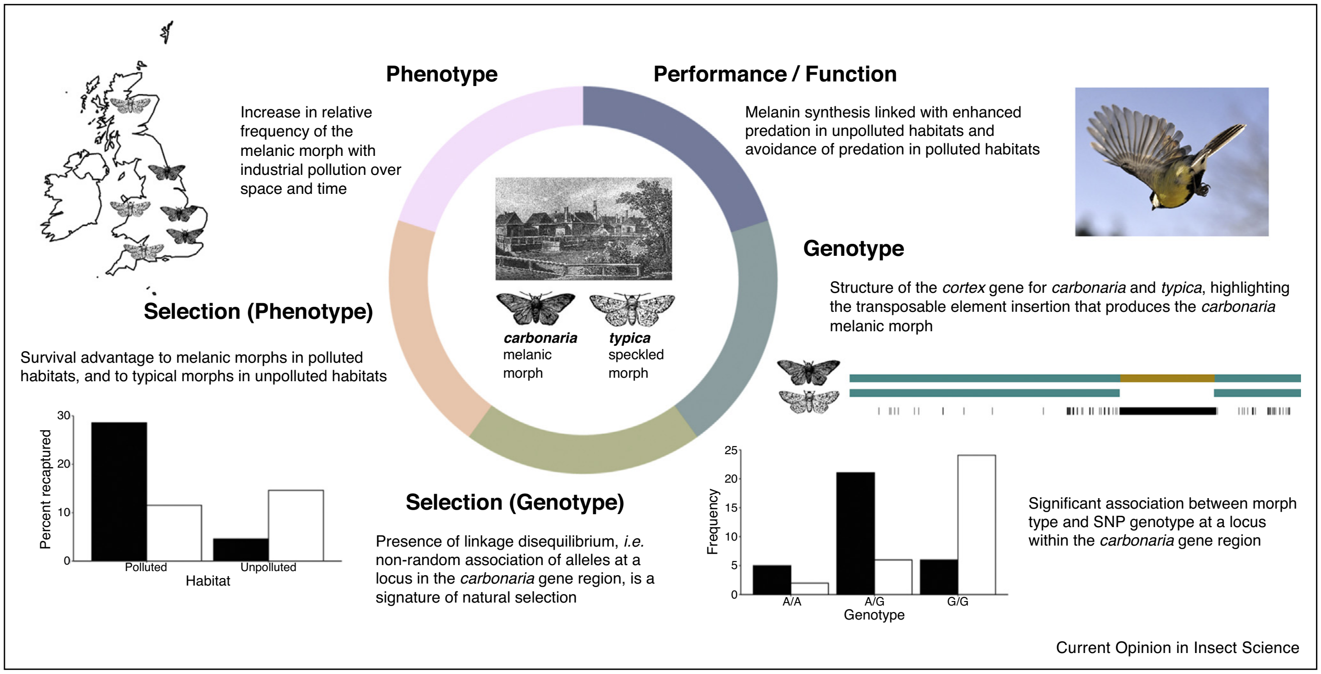
Building the case for urban adaptation with multiple lines of evidence, that is, using the hypothetico-deductive method. In cases where direct estimation of fitness across urban and rural environments is not measured, evidence for adaptive urban evolution can be developed through a combination of theory-based predictions and cross-taxa and cross-city comparisons. A recent study has taken this approach in urban Lepidoptera and their developmental responses to urban heat islands (UHI) and artificial light at night (ALAN) [8••]. Repeated evolution of a lower daylength threshold for direct development across multiple species and cities, which was predicted based on theory for UHI effects on development, provides evidence that these changes are adaptive responses to urban heat islands. Drawing of the butterfly *Pieris napi* (public domain) from Jacob Hübner's *Das kleine Schmetterlingsbuch*.

treatments within the common garden design can be used to partition plasticity and evolutionary divergence [4•,22]. It is important to bear in mind that either plasticity or evolution (including the evolution of plasticity) could be adaptive, though in different ways [22,23].

Molecular approaches have the main advantage of being an increasingly available tool for assessing urban adaptation across a broad range of organisms. For example, genomic analyses that detect loci under selection have been used to assess the evidence for urban adaptation from insects to large mammals [24–28]. However, there are also several limitations with this type of approach. For example, outlier-based analyses are susceptible to both false positives and negatives, and loci can be misclassified as being selected upon due to linkage disequilibrium or genetic drift [29]. Without separate or integrated phenotypic approaches, directly attributing allelic changes at the molecular level with adaptation to particular environmental selection pressures is necessarily indirect [30]. Further, while some study systems, such as the evolution of melanin in peppered moths in response to industrial pollution [31,32], yield evidence of changes in single loci of major effect (in this case, a large insertion within the *cortex* gene, resulting in increased melanization [33,34]; Figure 3), many traits that would be important in responding to urbanization are likely to be or known to be polygenic. The polygenic nature of many traits, such as heat tolerance, drought tolerance, and even pollution tolerance in other study systems, can make it difficult to detect evidence of selection at the genomic level when there are many genes each contributing a moderate amount to a given phenotype [35].

Study systems that integrate molecular data, phenotypic data, and fitness are still quite rare among those focused on urban adaptation [4•]. The peppered moth system (Figure 3) or the Atlantic killifish system are exceptions. In Atlantic killifish, survival of the populations that have evolved in response to urban pollution is much greater than unexposed killifish populations when challenged with increasing concentrations of the pollutant. These fitness differences have been linked with the repeated evolution of components of the aryl hydrocarbon receptor–based signaling pathway among different urban and non-urban paired populations [36]. There are both biological and methodological reasons for increasing the number of study systems that integrate these approaches. Biologically, the combination of the two approaches can be used to evaluate the hypothesis that parallel evolution will be greater at higher-order levels of biological organization (phenotypes) as compared with lower-order levels (genotypes) [37]. Methodologically, assessment of both approaches allows for ground-truthing of inferences from molecular analyses to directly link evolved changes of phenotypes with fitness.

Figure 3



Phenotype

Increase in relative frequency of the melanic morph with industrial pollution over space and time

Performance / Function

Melanin synthesis linked with enhanced predation in unpolluted habitats and avoidance of predation in polluted habitats

Genotype

Structure of the *cortex* gene for *carbonaria* and *typica*, highlighting the transposable element insertion that produces the *carbonaria* melanic morph

Selection (Phenotype)

Survival advantage to melanic morphs in polluted habitats, and to typical morphs in unpolluted habitats

Selection (Genotype)

Presence of linkage disequilibrium, *i.e.* non-random association of alleles at a locus in the *carbonaria* gene region, is a signature of natural selection

Significant association between morph type and SNP genotype at a locus within the *carbonaria* gene region

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Integration of phenotypic and molecular genetic approaches to understand the evolution of melanin in the peppered moth, *Biston betularia*, in response to industrial pollution. Image/data sources: map showing general patterns of phenotypic variation in melanism across spatial gradients in pollution (based on patterns from Ref. [32]); mark-recapture phenotypic selection data (redrawn using data from Ref. [31]); genotypic data (redrawn using data from Ref. [33]); structure of the *cortex* gene for the two morphs (solid horizontal bars) and candidate polymorphisms (short vertical lines) (redrawn using data from Ref. [33]); photo of *Parus major*, a common predator of peppered moths (Holger Uwe Schmitt via Wikimedia Commons); moth drawings (Encyclopedia Britannica 1911, public domain, via Wikimedia Commons); and steel mill drawing (Dillinger Hütte, public domain, via Wikimedia Commons).

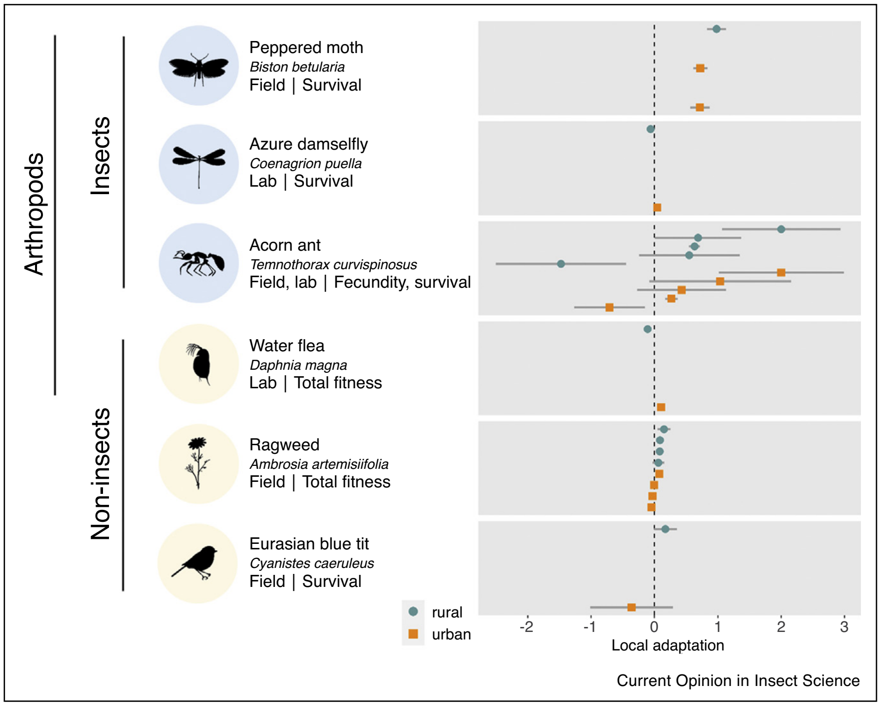
In the next section, we focus on assessing the evidence for urban local adaptation from phenotypic reciprocal transplant studies. We do this for two reasons: first, there are standard methods to make quantitative comparisons of local adaptation based on phenotypic data, and second, reciprocal transplantation studies that largely rely on phenotypic measurements of fitness are the most direct method to assess urban local adaptation [7].

Reciprocal transplants

To summarize the general patterns of urban local adaptation from reciprocal transplants, we consider traditional field reciprocal transplant studies as well as studies for which direct, ecologically relevant total fitness or components of fitness (either via survival or fecundity) of urban and rural populations was measured in urban-mimicking and rural-mimicking environments (e.g. laboratory common garden experiments). Because we were not only interested in assessing the evidence for urban and rural local adaptation, but also the potential costs of adaptation in the form of loss of adaptation to the ancestral environment, we excluded a small number of studies that performed one-way transplants, for example [38]. We also excluded a small number of studies that had multiple simultaneous manipulations, some of which were explicitly capturing urban-rural variation, and other manipulations that were not, for example [39]. There were 27 estimates of local adaptation, 13 in rural environments, and 14 in urban environments. These came from 7 studies, 4 of which involve insect systems (5, when considering arthropods), across 3 unique species (4, again, if considering arthropods) [13,14•,19,31,40–42] (Figure 4). Insects therefore make up a large fraction of the taxonomic diversity among urban-rural reciprocal transplant studies: half of the studies include insects, whereas the other half is split among plant, bird, and non-insect arthropod species.

We used local-foreign comparisons to quantify local adaptation [2], taking the relative fitness of the local population in their home environment (or home-mimicking treatment in the lab) minus the relative fitness of the foreign population in this same environment. This metric is an estimate of selection against migrants into a population with positive values indicating selection against migrants (i.e. local adaptation), and negative values indicating that migrants would have greater fitness than the local population (i.e. maladaptation of the local

Figure 4



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Estimates of local adaptation ± 1 SE from field and lab experiments measuring the fitness of urban and rural populations in urban and rural habitats and manipulated laboratory conditions. Local adaptation was quantified as $\frac{W_{population\ 1} - W_{population\ 2}}{\overline{W}_{environment\ 1}}$ where W represents the mean fitness of each population in environment 1 and $\overline{W}$ represents the mean fitness of all populations in environment 1. Results are grouped by species and ordered such that the three insect studies are at the top, followed by the one non-insect arthropod study, and the remaining two non-insect studies at the bottom. Positive values indicate greater relative fitness of the native population in comparison to the foreign population (i.e. adaptation) and negative values indicate greater fitness of the foreign population in comparison to the native population (i.e. maladaptation). Studies include: *Ambrosia artemisiifolia* [42], *Biston betularia* [31], *Cyanistes caeruleus* [40], *Coenagrion puella* [19], *Daphnia magna* [41], *Temnothorax curvispinosus* [13,14•]. Broadly representative taxonomic icons for each species were obtained from Phylopic (all public domain versions). Detailed study information and data available in Table S1 in Supplementary material.

population). We used a simple vote-counting approach to quantify the fraction of studies consistent with or divergent from expectations of local adaptation. There was a general signal of contemporary local adaptation: 64% of the estimates were consistent with urban local adaptation, and 77% were consistent with rural local adaptation (i.e. positive values). Each of the three insect systems showed evidence of local adaptation to urban environments. Except for the peppered moths that exclusively showed evidence of both urban and rural local adaptation, the remaining two insect study systems also showed some evidence of maladaptation, including in rural populations of the azure damselfly, and both urban and rural populations of the acorn ants (Figure 4).

The overall frequency of urban and rural local adaptation was comparable to broad-scale syntheses in other taxa and environmental contexts [2,43–48]. Yet the systematically weaker support for urban local adaptation compared with rural local adaptation suggests that urban populations are actually getting worse in the ancestral environment faster than they are improving in their own environment. As a specific example, acorn ants appear to be losing their cold tolerance to a greater degree than they are gaining heat tolerance in their evolutionary responses to urban heat island effects [13].

While it is evident that the rural populations have had more generations to evolve to their environment, it is an insufficient explanation for the considerable loss of adaptation of the urban populations to the ancestral rural environment. Rather, theory predicts that adaptation to a new environment can cause increasing fitness trade-offs to the ancestral environment [49–52]. This could explain the greater magnitude of fitness trade-offs for urban populations transplanted to their ancestral rural environment (Figure 4).

Importantly, fitness trade-offs across environments were not a uniform response among study systems, a finding consistent with other studies of local adaptation [2,53]. For example, some urban populations exhibited high fitness across both urban and rural environments (Figure 4). The presence of fitness trade-offs might therefore be modulated by features of the urban and rural environments. Costs of adaptation (i.e. trade-offs) are less likely to be exposed to selection in homogeneous environments [51,53], and thus divergence is more likely to result in fitness trade-offs across heterogeneous environments. Moving forward, exploring the features of the adaptive landscape within and across cities might help explain variation in how urban adaptation progresses in response to differing agents of selection.

Future prospectus

Understanding whether and how urban adaptation occurs has important implications for the long-term stability of insect populations in urban environments and under global climate change, especially as cities can be used as a proxy for future climate change [19]. Although cities often reduce biodiversity [54], they can sometimes maintain or even enhance biodiversity [55,56], a pattern that is especially common among insects [57]. Urban biodiversity can be maintained by unidirectional dispersal into cities, transient or migrating individuals, or repeated introductions to cities. Potentially for these urban dispersers, and especially for resident populations exposed to modified urban environments, evolution that confers a fitness advantage can be an important part of maintaining urban biodiversity.

The evidence so far suggests adaptive evolution is in progress in cities, but that broadly, many urban populations are likely still experiencing strong selection. In effect, there is asymmetry of local adaptation based on the population of origin, with urban local adaptation being less frequent than rural local adaptation. Although these are the general patterns, there is considerable variation in the magnitude and sometimes the direction of local adaptation (Figure 4). Future considerations targeted specifically at the role of environmental heterogeneity and the costs of adaptation might help to explain some of this variation.

There were a number of studies which did not meet our specific criteria for the synthetic analysis of local adaptation, but nonetheless provide important insights into urban adaptation, and point to fruitful areas of future research. For example, previous work suggested biotic interactions were some of the strongest drivers of phenotypic change in human-modified environments [58]. New research showing cryptic eco-evolutionary dynamics between water fleas and an insect predator provide the first explicit demonstration of these types of responses [59••]. Similarly, some of the strongest adaptive evolution in any environmental context is in response to applied selective pressures, such as pesticides [60], rather than the unintended consequences of urbanization such as urban heat islands. Recent work focused on the effects of pesticides on survival in cities [61] or in urban-adjacent agricultural contexts [62] support this pattern. In the future, it will be interesting to examine whether these types of selection pressures yield even greater magnitudes of local adaptation from what is already known from cities.

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Conflict of interest statement

Nothing declared.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.cois.2022.100893.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Siepielski AM, Morrissey MB, Buoro M, Carlson SM, Caruso CM, Clegg SM, Coulson T, DiBattista J, Gotanda KM, Francis CD *et al.*: **Precipitation drives global variation in natural selection**. *Science* 2017, **355**:959-962.

2. Hereford J: **A quantitative survey of local adaptation and fitness trade-offs**. *Am Nat* 2009, **173**:579-588.

3. Diamond SE, Martin RA: **Evolution is a double-edged sword, not a silver bullet, to confront climate change**. *Ann N Y Acad Sci* 2020, **1469**:38-51.

4. • Diamond SE, Martin RA: **Evolution in cities**. *Annual Review of Ecology, Evolution, and Systematics* 2021, **52**:519-540

This review article provides a summary of adaptive and non-adaptive evolution in cities with a particular focus on ways of designing urban evolution studies to appropriately detect urban adaptation and attribute changes to particular agents of selection.

5. • Lambert MR, Brans KI, Roches SD, Donihue CM, Diamond SE: **Adaptive evolution in cities: progress and misconceptions**. *Trends in Ecology and Evolution* 2021, **36**:239-257

This review lays out a set of criteria for assessing urban adaptation, and highlights different empirical case studies that meet these criteria.

6. • Szulkin M, Munshi-South J, Charmantier A (Eds): *Urban Evolutionary Biology*. Oxford University Press; 2020

This edited, multi-contributor book contains a number of chapters examining adaptive urban evolution from phenotypic and molecular perspectives, including chapters on parallel evolution, genomic signatures of urban adaptation, and biotic and abiotic agents of urban selection. Other chapters provide overviews of non-adaptive urban evolution (e.g. gene flow), though many also consider how these processes might interact with urban adaptation.

7. Johnson LC, Galliart MB, Alsdurf JD, Maricle BR, Baer SG, Bello NM, Gibson DJ, Smith AB: **Reciprocal transplant gardens as gold standard to detect local adaptation in grassland species: new opportunities moving into the 21st century**. *J Ecol* 2021 http://dx.doi.org/10.1111/1365-2745.13695. in press.

8. •• Merckx T, Nielsen ME, Heliölä J, Kuussaari M, Pettersson LB, Pöyry J, Tiainen J, Gotthard K, Kivelä SM: **Urbanization extends flight phenology and leads to local adaptation of seasonal plasticity in Lepidoptera**. *Proceedings of the National Academy of Sciences* 2021, **118**

This study combines long-term observations with common garden experiments to show the repeated evolution of seasonal timing in response to urban heat islands, rather than artificial light at night, across multiple Lepidopteran species and multiple cities. As such, this study provides evidence of urban adaptation to heat island effects.

9. Perrier C, Caizergues A, Charmantier A: **Adaptation genomics in urban environments**. *Urban Evolutionary Biology*. Oxford University Press; 2020:74-90.
10. Basset Y, Lamarre GPA: **Toward a world that values insects**. *Science* 2019, **364**:1230-1231.
11. Wright SJ, Goad DM, Gross BL, Muñoz PR, Olsen KM: **Genetic trade-offs underlie divergent life history strategies for local adaptation in white clover**. *Mol Ecol* 2021 http://dx.doi.org/10.1111/mec.16180. in press.
12. Lowry DB, Lovell JT, Zhang L, Bonnette J, Fay PA, Mitchell RB, Lloyd-Reilley J, Boe AR, Wu Y, Rouquette FM *et al.*: **QTL × environment interactions underlie adaptive divergence in switchgrass across a large latitudinal gradient**. *PNAS* 2019, **116**:12933-12941.
13. Diamond SE, Chick LD, Perez A, Strickler SA, Martin RA: **Evolution of thermal tolerance and its fitness consequences: parallel and non-parallel responses to urban heat islands across three cities**. *Proc R Soc B* 2018, **285**:20180036.
14. • Martin RA, Chick LD, Garvin ML, Diamond SE: **In a nutshell, a reciprocal transplant experiment reveals local adaptation and fitness trade-offs in response to urban evolution in an acorn-dwelling ant**. *Evolution* 2021, **75**:876-887

This field-based, multi-year reciprocal transplant in acorn ants study found evidence of urban and rural local adaptation via survival based on both local-foreign and home-away comparisons. Seasonal bias in mortality for ants transplanted into the away environment relative to ants transplanted to their home environment was consistent with the importance of evolved high temperature tolerance during summer in urban ants and the maintenance of low temperature tolerance over winter in rural ants.

15. Lande R, Arnold SJ: **The measurement of selection on correlated characters**. *Evolution* 1983, **37**:1210-1226.
16. Wade MJ, Kalisz S: **The causes of natural selection**. *Evolution* 1990, **44**:1947-1955.
17. Arnold SJ: **Morphology, performance and fitness**. *Am Zool* 1983, **23**:347-361.
18. Sinervo B, Basolo AL: **Testing adaptation using phenotypic manipulations**. *Adaptation*. Academic Press; 1996:149-185.
19. Tüzün N, Op de Beeck L, Brans KI, Janssens L, Stoks R: **Microgeographic differentiation in thermal performance curves between rural and urban populations of an aquatic insect**. *Evol Appl* 2017, **10**:1067-1075.
20. Diamond SE, Martin RA: **Physiological adaptation to cities as a proxy to forecast global-scale responses to climate change**. *J Exp Biol* 2021, **224**:jeb229336.
21. Kostanecki A, Gorton AJ, Moeller DA: **An urban–rural spotlight: evolution at small spatial scales among urban and rural populations of common ragweed**. *J Urban Ecol* 2021, **7**:juab004.
22. Ghalambor CK, McKAY JK, Carroll SP, Reznick DN: **Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments**. *Funct Ecol* 2007, **21**:394-407.
23. Diamond SE, Martin RA: **The interplay between plasticity and evolution in response to human-induced environmental change**. *F1000Res* 2016, **5**:2835.
24. DeCandia AL, Brzeski KE, Heppenheimer E, Caro CV, Camenisch G, Wandeler P, Driscoll C, vonHoldt BM: **Urban colonization through multiple genetic lenses: the city-fox phenomenon revisited**. *Ecol Evol* 2019, **9**:2046-2060.
25. Khimoun A, Doums C, Molet M, Kaufmann B, Peronnet R, Eyer PA, Mona S: **Urbanization without isolation: the absence of genetic structure among cities and forests in the tiny acorn ant *Temnothorax nylanderi***. *Biol Lett* 2020, **16**:20190741.
26. Mueller JC, Carrete M, Boerno S, Kuhl H, Tella JL, Kempenaers B: **Genes acting in synapses and neuron projections are early targets of selection during urban colonization**. *Mol Ecol* 2020, **29**:3403-3412.
27. Harpak A, Garud N, Rosenberg NA, Petrov DA, Combs M, Pennings PS, Munshi-South J: **Genetic adaptation in New York city rats**. *Genome Biol Evol* 2021, **13**:evaa247.
28. Salmón P, Jacobs A, Ahrén D, Biard C, Dingemanse NJ, Dominoni DM, Helm B, Lundberg M, Senar JC, Sprau P *et al.*: **Continent-wide genomic signatures of adaptation to urbanisation in a songbird across Europe**. *Nat Commun* 2021, **12**:2983.
29. Hoban S, Kelley JL, Lotterhos KE, Antolin MF, Bradburd G, Lowry DB, Poss ML, Reed LK, Storfer A, Whitlock MC: **Finding the genomic basis of local adaptation: pitfalls, practical solutions, and future directions**. *Am Nat* 2016, **188**:379-397.
30. Barrett RDH, Hoekstra HE: **Molecular spandrels: tests of adaptation at the genetic level**. *Nat Rev Genet* 2011, **12**:767-780.
31. Kettlewell HBD: **Further selection experiments on industrial melanism in the Lepidoptera**. *Heredity* 1956, **10**:287-301.
32. Kettlewell B: *Evolution of Melanism: the Study of a Recurring Necessity*. Clarendon Press; 1973.
33. Van't Hof AE, Edmonds N, Dalíková M, Marec F, Saccheri IJ: **Industrial melanism in British peppered moths has a singular and recent mutational origin**. *Science* 2011, **332**:958-960.
34. Van't Hof AE, Campagne P, Rigden DJ, Yung CJ, Lingley J, Quail MA, Hall N, Darby AC, Saccheri IJ: **The industrial melanism mutation in British peppered moths is a transposable element**. *Nature* 2016, **534**:102-105.
35. Barghi N, Hermisson J, Schlötterer C: **Polygenic adaptation: a unifying framework to understand positive selection**. *Nat Rev Genet* 2020, **21**:769-781.
36. Reid NM, Proestou DA, Clark BW, Warren WC, Colbourne JK, Shaw JR, Karchner SI, Hahn ME, Nacci D, Oleksiak MF *et al.*: **The genomic landscape of rapid repeated evolutionary adaptation to toxic pollution in wild fish**. *Science* 2016, **354**:1305-1308.
37. Santangelo JS, Miles LS, Breitbart ST, Murray-Stoker D, Rivkin LR, Johnson MTJ, Ness RW: **Urban environments as a framework to study parallel evolution**. *Urban Evolutionary Biology*. Oxford University Press; 2020:36-53.
38. Lambrecht SC, Mahieu S, Cheptou P-O: **Natural selection on plant physiological traits in an urban environment**. *Acta Oecol* 2016, **77**:67-74.
39. Tüzün N, Stoks R: **Lower bioenergetic costs but similar immune responsiveness under a heat wave in urban compared to rural damselflies**. *Evol Appl* 2021, **14**:24-35.
40. Capilla-Lasheras P, Dominoni DM, Babayan SA, O'Shaughnessy PJ, Mladenova M, Woodford L, Pollock CJ, Barr T, Baldini F, Helm B: **Elevated immune gene expression is associated with poor reproductive success of urban blue tits**. *Front Ecol Evol* 2017, **5**:64.
41. Brans KI, De Meester L: **City life on fast lanes: urbanization induces an evolutionary shift towards a faster life style in the water flea *Daphnia***. *Funct Ecol* 2018, **32**:2225-2240.
42. Gorton AJ, Moeller DA, Tiffin P: **Little plant, big city: a test of adaptation to urban environments in common ragweed (*Ambrosia artemisiifolia*)**. *Proc R Soc B* 2018, **285**:20180968.
43. Lortie CJ, Hierro JL: **A synthesis of local adaptation to climate through reciprocal common gardens**. *J Ecol* 2021 http://dx.doi.org/10.1111/1365-2745.13664. in press.
44. Greischar MA, Koskella B: **A synthesis of experimental work on parasite local adaptation**. *Ecol Lett* 2007, **10**:418-434.
45. Hoeksema JD, Forde SE: **A meta-analysis of factors affecting local adaptation between interacting species**. *Am Nat* 2008, **171**:275-290.
46. Leimu R, Fischer M: **A meta-analysis of local adaptation in plants**. *PLoS One* 2008, **3**:e4010.

47. Fraser DJ, Weir LK, Bernatchez L, Hansen MM, Taylor EB: **Extent and scale of local adaptation in salmonid fishes: review and meta-analysis**. *Heredity* 2011, **106**:404-420.

48. Sanford E, Kelly MW: **Local adaptation in marine invertebrates**. *Ann Rev Mar Sci* 2011, **3**:509-535.

49. Futuyma DJ, Moreno G: **The evolution of ecological specialization**. *Annu Rev Ecol Evol Syst* 1988, **19**:207-233.

50. Fry JD: **The evolution of host specialization: are trade-offs overrated?** *Am Nat* 1996, **148**:S84-S107.

51. Kassen R: **The experimental evolution of specialists, generalists, and the maintenance of diversity**. *J Evol Biol* 2002, **15**:173-190.

52. Schick A, Bailey SF, Kassen R: **Evolution of fitness trade-offs in locally adapted populations of *Pseudomonas fluorescens***. *Am Nat* 2015, **186(Suppl. 1)**:S48-S59.

53. Bono LM, Smith LB, Pfennig DW, Burch CL: **The emergence of performance trade-offs during local adaptation: insights from experimental evolution**. *Mol Ecol* 2017, **26**:1720-1733.

54. McDonald RI, Mansur AV, Ascensão F, Colbert M, Crossman K, Elmqvist T, Gonzalez A, Güneralp B, Haase D, Hamann M *et al.*: **Research gaps in knowledge of the impact of urban growth on biodiversity**. *Nat Sustain* 2020, **3**:16-24.

55. Des Roches S, Brans KI, Lambert MR, Rivkin LR, Savage AM, Schell CJ, Correa C, Meester LD, Diamond SE, Grimm NB *et al.*: **Socio-eco-evolutionary dynamics in cities**. *Evol Appl* 2021, **14**:248-267.

56. Shaffer HB: **Urban biodiversity arks**. *Nat Sustain* 2018, **1**:725-727.

57. Perez A, Diamond SE: **Idiosyncrasies in cities: evaluating patterns and drivers of ant biodiversity along urbanization gradients**. *J Urban Ecol* 2019, **5**:juz017.

58. Alberti M, Correa C, Marzluff JM, Hendry AP, Palkovacs EP, Gotanda KM, Hunt VM, Apgar TM, Zhou Y: **Global urban signatures of phenotypic change in animal and plant populations**. *PNAS* 2017, **114**:8951-8956.

59. •• Brans KI, Tüzün N, Sentis A, De Meester Stoks LR: **Cryptic eco-evolutionary feedback in the city: urban evolution of prey dampens the effect of urban evolution of the predator**. *J Anim Ecol* 2022, **91**:514-526

This study is one of the first to provide empirical support for urban eco-evolutionary feedbacks, specifically focusing on the evolution of predator–prey interactions between damselfly nymphs and water fleas in response to urban heat islands. In this case, urban predators showed higher encounter and predation rates compared with rural predators when exposed to rural prey, but urban and rural predators had similar responses when exposed to urban prey, indicating evolution of the predator to urbanization is masked by prey evolution.

60. Wada-Katsumata A, Silverman J, Schal C: **Changes in taste neurons support the emergence of an adaptive behavior in cockroaches**. *Science* 2013, **340**:972-975.

61. Brans KI, Almeida RA, Fajgenblat M: **Genetic differentiation in pesticide resistance between urban and rural populations of a nontarget freshwater keystone interactor, *Daphnia magna***. *Evol Appl* 2021, **14**:2541-2552.

62. Almeida RA, Lemmens P, De Meester L, Brans KI: **Differential local genetic adaptation to pesticide use in organic and conventional agriculture in an aquatic non-target species**. *Proc R Soc B* 2021, **288**:20211903.