

Opinion

Speciation and the City

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Many outstanding questions about speciation are difficult to test empirically because of a lack of suitable study systems. Here, we highlight studies of evolutionary ecology in urban environments to argue that cities provide ideal conditions that can be leveraged to study the speciation process. Considering general findings from these studies, we discuss the mechanisms of speciation that are likely to occur in cities. We also discuss fundamental questions about speciation that urban environments are uniquely suited to address, such as those about the earliest stages of divergence or the role of phenotypic plasticity. We conclude that the study of contemporary speciation in urban environments has promise to facilitate discoveries about the process of speciation as it occurs in the Anthropocene.

Empirical Studies of Speciation and the Utility of Urban Environments

Speciation (see [Glossary](#)) is the evolutionary process that generates reproductively isolated groups of organisms we call species. In documenting the processes that lead to the origin of species, biologists gain insight into the evolutionary mechanisms that generate biological diversity [1] and structure ecological communities [2]. Many empirical questions about speciation are best addressed via the study of wild populations, but progress is limited by our ability to identify suitable model systems in which to generate and test our predictions (see [3] for a list of outstanding questions about speciation). One such question, for example, is: what are the reproductive isolating barriers that evolve first during speciation? In order to address this question, it is necessary to identify populations that are in the initial stages of divergence (e.g., [4]). Here, we argue that urban environments provide ideal conditions for several mechanisms of speciation and are a likely source of study systems with which to test fundamental empirical questions about the process. We conclude that studying the process of speciation in urban environments has promise to both refine our understanding of established mechanisms of speciation and to facilitate advances in areas of research where progress has been limited.

Potential for Speciation in Urban Environments

Evolutionary Ecology of Urban Environments

Urbanisation – the conversion of natural landscapes into human settlements – is an ongoing global process. Distinct urban environments, while exhibiting some heterogeneity within and between them, have many features in common. For example, urban environments are generally warmer [5] and more fragmented [6] than nearby nonurban environments. Relative to other types of anthropogenic land-use change – such as deforestation or mining – urban environments are unique because they are generally permanent; there is no analogue to reforestation or mine reclamation for cities. When we refer to urban environments in this article we are typically envisioning large and densely populated settlements. We note that similar ecological and evolutionary processes have been documented in towns with populations in the tens of thousands and in cities with populations in the millions [5,7], suggesting that the processes we describe herein can apply to human settlements generally and not just cities. Last, we emphasise that urbanisation is an ongoing and spatially variable phenomenon and urban environments are therefore best viewed as dynamic environmental gradients rather than static and discrete patches.

Highlights

Urban environments likely promote speciation through several mechanisms.

Features of cities make them ideal for studying outstanding questions about speciation.

Data testing hypotheses about speciation in cities are scarce.

Studying urban speciation will improve our understanding of speciation in the Anthropocene.

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The available evidence supports the hypothesis that the ecological features of urban environments can affect various evolutionary processes in urban-dwelling natural populations. Studies have documented divergent selection and/or phenotypic evolution between urban and nonurban environments, higher mutation rates in urban populations, and have found that urbanisation alters migration regimes and the strength of genetic drift [8]. Although speciation is a major area of research in evolutionary biology, studies on evolutionary processes in cities tend not to consider questions about speciation.

Evidence for (Nonurban) Contemporary Speciation

Recent advances in our understanding of the rate at which reproductive isolation can evolve suggest that progress toward speciation in cities ought to be observable on contemporary timescales. Several studies have documented the rapid evolution of reproductive isolation in natural populations [9], and speciation rates might be accelerating due to human activities [10]. Most documented cases of contemporary speciation have been associated with exotic species. Introduced species can drive speciation if they create a new ecological niche – such as a novel host-plant resource – that facilitates divergence among native species [11], or if they can form new species by hybridising with previously allopatric native species [12]. In addition to speciation associated with species relocations, biologists have documented several cases of rapid – and in some cases complete – speciation caused by anthropogenic land-use changes other than urbanisation (Box 1). Rates of recent phenotypic change seem to be greater in urban areas than in any other habitat type, including nonurban anthropogenic contexts [13],

Box 1. Cases of Speciation Caused by Anthropogenic Environmental Change

Human activities can promote speciation [9,14]. Here, we briefly highlight several examples that illustrate how anthropogenic land use changes, other than urbanisation, have inadvertently contributed to the evolution of reproductive isolating barriers. Speciation is complete in some cases, and underway in others.

Scientists have identified several cases wherein adaptation to mine tailings spurred the evolution of reproductive isolation. In these examples, the transition from natural to polluted soil generates divergent selection. Following adaptation to the toxic soil conditions, adaptive differentiation in flowering time reduces gene flow between parapatric populations [69]. Alternatively, studies have identified cases where strong reproductive isolation between mine and nonmine populations evolved as a byproduct of adaptation for copper tolerance [70] because of linkage between a locally adaptive allele and an allele that causes hybrid lethality [71].

Anthropogenic habitat fragmentation has been shown to impact gene flow directly in several native species. For example, deforestation in Central America has led to a complete cessation of gene flow between populations of the rainforest damselfly, *Megaloprepus caerulatus*, rendering them independent evolutionary lineages [72]. The construction of a freeway in California, USA, caused the isolation and subsequent genetic differentiation between populations of mammalian carnivores on opposite sides [73]. We note that while fragmentation clearly reduces gene flow, its ability to cause speciation is ultimately contingent on the evolution of genetically based isolating barriers and the persistence of remnant populations [74]. Geographic isolation is an important first step in such a process.

Human landscape alteration has led to new species arising through hybridisation. An example of this is in sculpin fish, where the construction of canals connected previously separate waterways and brought two historically allopatric species into contact. The evidence suggests that species hybridised and formed a new homoploid hybrid species that is isolated from its parents [75]. Importantly, some cases of hybridisation following human-caused landscape change can ultimately lead to the collapse of parent species if the new environment completely disrupts mating barriers or favours hybrids over parents [76]. It is possible that species fusion – collapse of previously isolated species into a hybrid swarm – is a more common result than hybrid speciation following human-caused landscape disturbance [77].

These studies collectively demonstrate that human-caused landscape change can cause speciation on contemporary timescales. Urbanisation alters environments in much the same way – by polluting, fragmenting, and restructuring natural landscapes – and thus has similar potential to cause speciation.

Glossary

Artificial speciation: species created by artificial selection, for example by breeding.

Autopolyploid: polyploid formed by genome duplication within a single lineage.

Allopolyploid: polyploid formed by duplication of a hybrid genome.

Commensal species: wild species that associate with human settlements; also known as synanthropes.

Contemporary speciation: speciation occurring over timescales of years to decades, rather than millennia.

Divergent selection: form of natural selection that favours distinct phenotypes in different environments.

Effective population size: size of an idealised population that experiences genetic drift with the same strength as the focal population; lower values indicate a higher strength of drift.

Gene flow: sharing of genetic material between groups.

Genetic drift: change in allele frequencies caused by random sampling error.

Homoploid hybrid speciation: species formed by hybridisation between two parental lineages without a change in ploidy.

Isolation-by-distance: neutral genetic divergence caused by limited dispersal between geographically distant populations.

Natural population: population that persists without intentional human assistance. Agricultural, horticultural, or laboratory populations are not natural populations.

Parallel speciation: independent evolution of the same mechanism of reproductive isolation in response to similar environmental conditions – typically a result of natural selection.

Reinforcement: evolution of isolating barriers in response to selection against intertype mating.

Reproductive isolation: genetically based barriers to gene flow between taxa.

Speciation: evolution of genetically based reproductive isolating barriers between lineages.

Synthetic speciation: onset of reproductive isolating barriers created with the aid of biotechnology.

suggesting that the environmental disturbances leading to human-mediated speciation might be particularly potent in cities.

Defining Urban Speciation

We define urban speciation as: the incidental and contemporary evolution of reproductive isolating barriers caused by the environmental conditions associated with urban environments. We stress that, given the short timespans involved, it is unlikely that cases of urban speciation will be complete. Rather, we focus on progress toward speciation rather than the completion of the process. Our definition of urban speciation includes speciation by genetic drift if features of urbanisation, such as fragmentation, reduce effective population size or simply reduce migration among populations. Urban speciation can be considered a subcategory of human-mediated speciation [14] and we exclude cases of artificial and synthetic speciation [15], which are not always incidental. Throughout the article, we discuss speciation as it proceeds in eukaryotic and sexually reproducing populations.

Evidence for Urban Speciation

While there are relatively few case studies, compelling evidence suggests that speciation is ongoing in urban environments. The strongest evidence that new species can originate in urban environments comes from the London Underground mosquito where complete reproductive isolation appears to have evolved between ancestral surface and derived underground populations [16], although some important uncertainties remain (Box 2). Several studies have documented sharp breaks in gene flow between urban and adjacent nonurban populations but do not explicitly quantify isolating barriers. For example, two species of African malaria mosquito form genetically differentiated populations in urban and rural areas, possibly mediated by divergent selection for pollutant and insecticide resistance [17]. In addition, at least three species seem to have originated in urban environments by hybridisation (discussed below). Commensal species provide further support for the hypothesis that urban environments can promote speciation because dozens of taxa are associated only with urban environments [8], and some commensals are reproductively isolated from their extant non-commensal relatives [e.g., bedbugs (*Cimex lectularius* [18])]. Additional studies, discussed below, demonstrate that many taxa are undergoing phenotypic and genetic divergence in response to urbanisation.

Our central argument is that urban speciation is plausible, and that several lines of evidence support the claim that progress toward speciation is ongoing and observable in cities. While the strength of evidence in support of putative cases of urban speciation can – and should – be debated, the reality is that there is a lack of data available to robustly evaluate hypotheses about speciation in cities. That is, the lack of compelling case studies of urban speciation could reflect an absence of attention rather than an absence of process. The most obvious issue is that studies of evolution in urban environments do not apply standardised methods for quantifying the strength of reproductive isolation between populations (see [19]). To this end, we suggest that three criteria be met in future studies that aim to conclusively test hypotheses about urban speciation (Table 1). In the next section, we discuss the speciation process as it might occur in cities.

Mechanisms of Speciation in Urban Environments

The environmental conditions associated with urbanisation have the potential to promote speciation through several mechanisms (Figure 1). Here, we connect emerging results from studies of urban evolutionary ecology with theory on mechanisms of speciation and highlight

Urban environment: human settlement, a subcategory of anthropogenic habitat disturbance; includes cities, towns, and villages.
Urbanisation: transformation of a natural landscape into an urban environment (see Urban environment).

Box 2. Urban Speciation in the London Underground Mosquito

Although much work remains to be done, the best-supported case consistent with the process of urban speciation is that of the London Underground mosquito, *Culex pipiens f. molestus* (hereafter *C. molestus*) (Figure 1). This species is found in the tunnels below London, UK, and is closely related to the aboveground species, *C. pipiens*. Because the Underground opened in the 1860s, divergence between the forms seems to have arisen in <150 years. Based on the criteria in Table 1 (see main text), this species provides a compelling case of urban speciation.

Byrne and Nichols [16] sampled several populations of both *C. molestus* and *C. pipiens* and demonstrated significant genetic structure that separate their sampled populations into two main genetic clusters. The authors found that the genetic clusters are specifically associated with the novel urban habitat (underground) and the ancestral (surface) habitat, and effectively ruled out isolation by distance as the primary cause of divergence (criterion 1). These genetic data are consistent with the hypothesis that the underground population is derived from a small population of *C. pipiens* that colonised the underground from the surface (criterion 2).

Byrne and Nichols [16] documented several traits for which the surface and underground species have diverged. *C. pipiens* is adapted to feed on birds, whereas in the largely bird-free underground, *C. molestus* is adapted for mammal feeding. Because food is less plentiful in the underground, *C. molestus* has adapted to oviposit without a blood meal. Underground populations no longer undergo diapause during winter because warmer year-round temperatures in the underground negate the need for this. Crosses among surface populations, and among underground populations, have all resulted in viable and fertile offspring. Crosses between surface and underground populations, however, typically have failed to produce viable offspring, and viable offspring are sterile. The phenotypic shifts are consistent with divergent selection contributing to ecological speciation. The mechanisms causing hybrid inviability and sterility (criterion 3) have not been determined.

We stress that some remaining ambiguities preclude the assertion that the London Underground mosquito is a *bona fide* case of urban speciation. It would be valuable for future work on this system to further resolve the ecological and genetic mechanisms that contribute to reproductive isolation. In addition, although existing data from allozymes support the hypothesis that *C. molestus* is derived from the local *C. pipiens* population, the application of modern molecular genetic techniques to the London Underground mosquito would be useful for robustly estimating its time of origin (see [78,79]).



Figure 1. *Culex pipiens f. molestus*. Photo: Martin Olofsson.

the geographic context in which these mechanisms are best studied. In addition, we suggest several questions that could be addressed to test the hypotheses outlined below (see Outstanding Questions).

Ecological Speciation

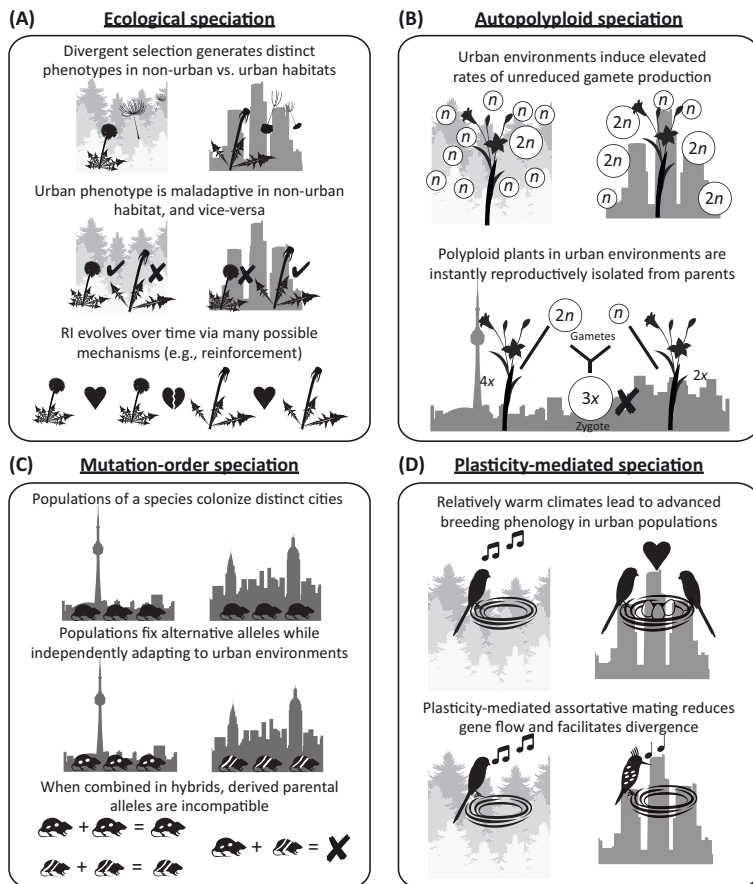
Divergent selection can drive the origin of species as a consequence of adaptation to contrasting environments – a process referred to as ecological speciation [20]. This process might

Table 1. Necessary Criteria to Demonstrate Urban Speciation

Criterion	Rationale	Example test and result	Exceptions	Comments
Gene flow between populations is associated with differences in their environments	If divergence is truly caused by urbanisation, expect greatest divergence between urban vs nonurban populations, and less between distinct urban populations	Compare nonurban vs nonurban populations and urban vs urban populations (if comparison of interest is urban vs nonurban populations), and demonstrate reduced differentiation between populations in similar habitats	If the evolution of RI is primarily caused by chance processes (e.g., mutation-order speciation) or intrinsic and/or chromosomal incompatibilities (e.g., polyploidy), then genetic divergence is not expected to be associated with differences in habitat conditions	These analyses are most effective if they control for isolation-by-distance in the sampling design (e.g., make urban vs urban and urban vs nonurban comparisons where populations are separated by similar geographic distances) Sampling multiple localities is essential because, when comparing a single pair of urban and nonurban populations, it is impossible to rule out isolation-by-distance as the sole cause of neutral divergence
Divergence is caused by urbanisation	Populations of interest might have diverged long before urbanisation began	Use DNA or propagules from museum and/or herbarium specimens to demonstrate that divergence began or accelerated recently	None	Incomplete RI might have existed before urbanisation and the role of urban environments could be to push speciation further toward completion
Mechanism of reproductive isolation is associated with urbanisation	Identify the specific manner through which urbanisation has contributed to the evolution of isolating barriers	If hypothesis is 'ecological speciation': present evidence of reciprocal selection against immigrants (i.e., transplant urban individuals in nonurban habitats, and vice versa), and demonstrate that divergence of maladaptive characters evolved by divergent natural selection	None	While correlational data are valuable, it will be necessary to measure organisms and conduct experiments in the field to conclusively test hypotheses

be associated with urbanisation because divergent natural selection can favour distinct phenotypes in adjacent urban and nonurban environments (Table S1 in the supplemental information online). Several case studies suggest that reproductive isolating barriers can evolve as a byproduct of adaptation to urban environments. For example, adaptation of beak traits in an urban population of house sparrows (*Carpodacus mexicanus*) in Arizona, USA, indirectly causes differences in courtship song between urban and nonurban populations, which are now diverging genetically [21]. Evolution of short dispersal distance in response to urban habitat fragmentation in the plant *Crepis sancta* [6] is expected to reduce migration of urban genotypes into nonurban habitats. Urban acorn ant (*Temnothorax curvispinosus*) populations have locally adapted thermal tolerances [22] and poor performance in alternative habitats could lead to reciprocal selection against immigrants (see [23]). Additional studies provide evidence for the genetic signature of ecological speciation (Table S1 in the supplemental information online). For example, urban populations of the Natal multimammate mouse (*Mastomys natalensis*) have diverged from surrounding rural populations within the past 150 years in spite of high gene flow, implicating strong divergent selection as the cause [24]. Studies that quantify the strength of isolating barriers associated with divergent natural selection are necessary to test hypotheses about ecological speciation in urban environments.

In addition to divergent natural selection, divergent sexual selection between environments can spur ecological speciation [25]. Although there are few studies on the subject, the available evidence supports the hypothesis that sexual selection can differ between urban and nonurban environments, potentially leading to some premating isolation. The strongest evidence comes from an urban population of dark-eyed juncos (*Junco hyemalis*), which have evolved 22% less



Trends in Ecology & Evolution

Figure 1. Mechanistic Hypothetical Examples of Progress toward Speciation in Urban Environments. (A) Divergent natural selection leads to the evolution of distinct multivariate phenotypes (ecotypes) in urban and nonurban areas – each maladapted in the alternative environment. If hybrids are unfit in either parental environment selection against interecotype mating can eventually lead to the evolution of RI. (B) Parallel natural selection (here for white patterning phenotype) in cities leads to fixation of alternative adaptive alleles (here spots vs. stripes) by chance because stochastic factors influence the order in which they arise and fix. These two alleles can lead to extrinsic or intrinsic incompatibilities when combined in hybrids. (C) The conditions of urban environments might cause errors in plant meiosis, which leads to more unreduced gametes and subsequent formation of autopolyploids. Polyploids are instantly reproductively isolated from parents and, if they can persist, can be considered distinct species. (D) Advanced phenology in urban environments might lead to assortative mating between urban and nonurban populations, which then facilitates divergence in response to selection. Abbreviation: RI, reproductive isolation.

white colouration in tail feathers relative to nonurban populations because of altered sexual selection in the urban environment [26], although we note the mechanism linking urbanisation to altered sexual selection is unresolved. It is not clear whether urbanisation frequently alters sexual selection, and future studies should aim to determine whether divergent sexual selection and secondary sexual characteristics contribute to premating isolation between urban and nonurban populations.

Mutation-Order and Drift-Based Speciation

In contrast to divergent selection, parallel natural selection can drive speciation if different populations fix alternative, incompatible, advantageous alleles by chance when adapting to

similar environments. This process of mutation-order speciation is expected to occur primarily with low or absent gene flow [27] and could contribute to speciation between allopatric urban populations (Table S2 in the supplemental information online). For example, burrowing owls (*Athene cunicularia*) have independently colonised three Argentinian cities and, due to population bottlenecks, now possess different subsets of ancestral standing variation from which adaptation could proceed [28]. Similar processes can occur between spatially isolated remnant populations within the same city derived from a formerly unfragmented population. For example, remnant populations of the eastern water dragon (*Intellagama lesueurii*) in Brisbane parks exhibit high neutral divergence (mean $F_{ST} = 0.19$) despite being proximate and only recently separated by habitat fragmentation [29]. To the extent that urban environments exhibit parallel natural selection, cities might be an unintentional experiment in which to test questions about mutation-order speciation.

Reproductive isolation could also evolve between isolated urban populations in the absence of selection. Drift is elevated in urban populations of many species [8], and therefore isolated populations might fix unique deleterious or neutral mutations that are incompatible in hybrids. We suspect that a pure drift mode of urban speciation is unlikely, or at the least will be slower compared to other mechanisms. Nevertheless, interactions between drift and selection could be important for driving urban speciation.

Autopolyploid Speciation

Urban environments might be associated with autopolyploid speciation. Autopolyploid speciation is most common in plants and occurs following the union of two unreduced ($2n$) gametes from conspecific diploid parents [30]. Factors that increase $2n$ gamete production, such as temperature stress [31], often differ between urban and nonurban areas and thus could affect rates of $2n$ gamete production. Although polyploid species are over-represented relative to diploids in disturbed habitats compared with undisturbed habitats [32], little is known about the extent and origin of autopolyploidy in urban environments.

Allopolyploid and Hybrid Speciation

Allopolyploid and homoploid hybrid speciation could be relatively frequent in cities if hybridisation rates are elevated or if urban environments are favourable to the establishment of hybrids (Table S3 in the supplemental information online). Hybridisation between sympatric species is most frequent in disturbed habitats [33], and increased rates of hybridisation can spur diversification through the formation of hybrids between previously allopatric native and exotic taxa [12]. Such opportunities for novel hybridisation likely abound in cities, because exotic species are more common in cities than in natural or agricultural areas [34]. Indeed, humans seem to be accelerating rates of plant speciation via increased relocation of species, and hybrid species are typically first discovered in or near cities [10]. For example *Senecio cambrensis* and *Senecio eboracensis* both originated in British cities: *S. cambrensis* independently in both Edinburgh and Wrexham, and *S. eboracensis* in York [35]. The persistence of hybrid species is most likely when a novel environment is available for colonisation [36]. Urban habitats are notably heterogeneous [37] and therefore cities could be a favourable setting for the establishment of novel hybrid populations. Thus, while hybrid or allopolyploid speciation can occur anywhere, it might be particularly common in urban environments.

Direct Effects of Urbanisation on Gene Flow

Features of urban environments can reduce gene flow between populations. For example, native mice in New York City do not readily migrate between habitats separated by impervious surfaces and are undergoing genetic divergence as a result [38]. Some urban bird populations

cease winter migration and are adapting to a sedentary life history [39], which might contribute to genetic divergence between urban and nonurban populations [40]. In plants, changes in pollinator communities between urban and nonurban environments [41] could affect gene flow across habitats. Perhaps because of reduced pollinator density, urban plant communities exhibit higher self-compatibility than nonurban communities [34] and rates of self-fertilisation can be higher in urban plants [42]. Self-fertilisation reduces gene flow between populations, and might indirectly lead to assortative mating if floral traits and phenology evolve in association with mating system [43]. (Self-fertilisation could also evolve by reinforcement if there is selection against mating between urban and nonurban populations [44].) These direct effects of urbanisation on gene flow are expected to promote speciation via all mechanisms discussed above.

Using Urban Environments to Address Fundamental Questions about Speciation

While cities might provide study systems with which to refine our understanding of various speciation mechanisms, they offer a unique opportunity to test outstanding questions about speciation. Some questions, such as those about drift-selection interactions, reinforcement, or the genetic basis of reproductive isolation, are perhaps just as well suited to testing in urban environments as elsewhere. Here, we highlight the utility of urban environments for addressing fundamental questions about speciation that are difficult to study under many circumstances.

Early-Evolving Reproductive Barriers

The reproductive isolating barriers acting between species today did not necessarily cause speciation in the first place [45]. Rather, the most relevant barriers for speciation are those that evolve first, and biologists have developed many approaches to assess chronological patterns in the evolution of isolating barriers using taxa that vary in their time since divergence [1,4]. While such approaches are valuable, they often make use of taxa that already exhibit considerable divergence and have ambiguous phylogeographic histories. Speciation in response to urbanisation is necessarily recent, and because cities typically have a known time of founding, it is possible to precisely estimate when and where speciation began. Thus, studying urban speciation will identify the isolating barriers that evolve earliest during divergence.

Role of Plasticity in Speciation

Quantifying the importance of phenotypic plasticity for speciation is an active area of research [46]. The persistence of urban populations likely depends, to some degree, on plasticity, and thus the existence of plasticity could be relevant for most cases of urban speciation. Our discussion of plasticity here highlights two apparently general patterns of plasticity in cities that might be especially relevant for promoting progress toward speciation.

Perhaps the most well-studied plastic response to urbanisation is a shift in breeding phenology. At least in temperate regions, populations of birds and plants in cities generally initiate breeding before nonurban populations, possibly caused by increased temperature [47,48] and/or artificial lighting [49] in cities. Plastic variation in phenology caused by urbanisation is expected to reduce gene flow between habitats and facilitate a response to divergent selection [50]. Thus, the degree to which phenology is influenced by urbanisation could affect the rate of adaptive divergence between urban and nonurban populations.

In addition to phenology, another well-studied plastic difference between urban and nonurban habitats is in mating vocalisations [51]. In cities, courtship songs are drowned out by low-frequency anthropogenic noise, and this leads some birds and frogs to sing at higher frequencies in urban environments [52,53]. A playback experiment in European blackbirds (*Turdus*

merula) found that urban birds respond most strongly to urban songs, and forest birds respond most strongly to forest songs [54], providing suggestive evidence for assortative mating [55]. Cultural evolution of song in urban environments – where only effectively transmitted songs are copied – could accelerate divergence between urban and nonurban populations [56]. Song divergence might be accelerated in birds with learned, as opposed to innate, song if individuals raised in an urban area possess an urban song that persists even when they disperse to nonurban habitats [57]. Studies testing whether the effects of urbanisation on mating vocalisations lead to habitat-based assortative mating will improve our understanding of whether and how plastic behavioural change contributes to speciation.

Repeatability of Speciation

While examples of repeated adaptation abound [58], less is known about the repeatability of speciation. Cases of parallel speciation are valuable because their replication provides a unique opportunity to understand the conditions that are both necessary and sufficient for speciation to occur [59,60]. Given the widespread global replication of urbanisation, different cities might represent independent opportunities for speciation. Parallel allopolyploid speciation occurred in two distinct urban environments in *S. cambrensis* [35], although it is unclear if the parallel species – one of which is now extinct – were reproductively compatible. While ecological speciation has not yet been conclusively documented in cities, it is becoming clear that cities can drive independent, recurrent, divergent evolution between parapatric urban and nonurban populations (Table S1 in the supplemental information online). This result suggests that ecological speciation, if it occurs, has the potential to recur in distinct cities.

Perspectives, Caveats, and Future Directions

An important advance since the Modern Synthesis is the realisation that significant evolutionary change can occur over short timescales [58]. The recognition that adaptation can occur rapidly has inspired evolutionary biologists to generate and test hypotheses about the process as it happens in nature; for example, by tracking adaptation in invasive species [61]. In contrast to adaptation, biologists typically do not test predictions about speciation on contemporary timescales. We argue that the collective body of theory on speciation, paired with the evidence emerging from studies of urban evolutionary ecology, justify the prediction that contemporary speciation is likely ongoing in cities.

The timescale of urban speciation is unresolved. In some taxa where speciation seems to require hundreds of thousands of years (e.g., birds [62]), cities might simply be too recent to be causing appreciable progress toward speciation. Despite a possible lag before the evolution of complete reproductive isolation, it is possible to quantify the evolution of isolating barriers at any stage of divergence. Evolutionary biologists studying urban systems are now beginning to quantify the extent of local adaptation, patterns of assortative mating, barriers to gene flow, and the extent of genetic differentiation among populations. The next challenge is to explicitly quantify the strength of reproductive isolating barriers [19] to place these studies in a context where they can be compared to other studies of speciation.

Where Should We Look for Urban Speciation?

Rates of speciation are variable among environments and taxa. *In situ* speciation is more frequent on large islands [63] and in large lakes [64] compared to smaller islands and lakes. In large cities, greater distance between urban and nonurban populations, stronger natural selection, larger population sizes and/or a greater number of spatially distinct urban populations, might all facilitate speciation. All else being equal the process of urban speciation is likely to be further along in older cities. With this in mind, studies in large and old cities might find the greatest progress toward urban speciation.

Some taxa are more likely to undergo urban speciation than others. Species with limited migration and short generations can evolve reproductive isolation most quickly, and studies on short-lived invertebrates and plants are ideal candidates, although patterns consistent with ecological speciation in urban environments have been observed in organisms of widely varying life histories (Table S1 in the supplemental information online). Polyploid and/or hybrid speciation – where reproductive isolation can evolve instantaneously – could be frequent in cities and warrants immediate investigation.

Hypothesis-based natural history observations are a useful first step for identifying study systems and guiding research. For example, predictions about the evolution of self-compatibility in urban environments have been addressed by studying changes in floral morphology and pollination in natural populations along an urbanisation gradient [65]. Such descriptive studies facilitate the genesis of specific predictions about speciation in urban environments.

What Could Prevent Urban Speciation?

While many lines of evidence are consistent with urbanisation driving speciation, some features of cities could inhibit divergence. First, many features of urban environments change rapidly as culture and technology change and the human population grows. Such changes could limit the likelihood of speciation if they reduce population persistence or generate inconsistent selection. Second, some species migrate freely within and among cities – mediated by humans or by innate dispersal – causing derived advantageous alleles to become widespread and thus slowing the progress of mutation-order speciation or divergence via drift. Third, because urbanisation typically represents a gradient from low to high density, it is possible that populations could evolve stable clines (e.g., [7]) rather than sharp breaks in gene flow (e.g., [17]). Last, plasticity in urban environments could hinder speciation if it weakens divergent selection or assortative mating [66].

Concluding Remarks

A research programme on urban speciation has promise to complement ongoing research on speciation. An effort to identify ongoing urban speciation events will advance our understanding of speciation generally by providing systems with which to study the progression of rapid, contemporary, and parallel speciation. There are many outstanding questions about speciation as it occurs in urban environments (see Outstanding Questions), and addressing these questions will provide a solid foundation for research on urban speciation. Human activities are causing widespread extinctions and extirpations [67] and biodiversity losses will almost certainly far outpace any gains through contemporary speciation, especially with respect to phylogenetic diversity. Urbanisation itself is a contributor to the ongoing extinction crisis [68]. Nevertheless, whether, and through what mechanisms, anthropogenic environmental change can promote the evolution of new species is poorly understood [3] and studying urban speciation could facilitate progress on this issue. Although theories about speciation and data on urban evolutionary ecology align to support a prediction of urban speciation, and emerging patterns are consistent with this prediction, more data are needed to appraise the hypothesis that urban environments promote speciation in the Anthropocene.

Note Added In Proof

While this article was in press, an article was published reporting that the house sparrow (*Passer domesticus*) split from its non-commensal relative approximately 11 Kya and that the diverged genetic regions were associated with a novel high-starch diet [80]. The timing of this split occurred around the same time that humans began living in dense settlements and cultivating plants for consumption [81].

Outstanding Questions

Ecological speciation

Are phenotypes favoured by selection in urban environments typically maladaptive in nonurban environments (and vice versa)? That is, are urban populations locally adapted?

Is self-fertilisation or asexual reproduction favoured by selection in urban environments?

Does sexual selection differ between urban and nonurban environments? If so, does this lead to assortative mating between urban and non-urban populations?

Mutation-order speciation

How common is parallel genetic evolution in distinct populations of a species adapting to urban environments? For cases in which alternative advantageous mutations are fixed, are there fitness costs when they are combined in hybrids?

Autopolyploid speciation

Is the degree of unreduced gamete formation and autopolyploid speciation influenced by urbanisation?

Do the ecological conditions associated with urbanisation favour the persistence of polyploids over diploids?

Allopolyploid and hybrid speciation

How common is hybridisation in urban environments relative to other disturbed habitat types?

Is allopolyploid speciation more common in urban environments than non-urban environments?

Plasticity and speciation

Do plastic shifts in phenology reduce gene flow between urban and nonurban populations?

Does plasticity in mating vocalisation cause to pre-mating isolation between urban and nonurban populations?

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Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.tree.2018.08.007>.

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