Review

Phenotypic variation in urban environments: mechanisms and implications

M.J. Thompson,[1,2,*,@] P. Capilla-Lasheras,[3,@] D.M. Dominoni,[3,4,@] D. Réale,[1,@] and A. Charmantier[2,5,@]

In the past decade, numerous studies have explored how urbanisation affects the mean phenotypes of populations, but it remains unknown how urbanisation impacts phenotypic variation, a key target of selection that shapes, and is shaped by, eco-evolutionary processes. Our review suggests that urbanisation may often increase intraspecific phenotypic variation through several processes; a conclusion aligned with results from our illustrative analysis on tit morphology across 13 European city/forest population pairs. Urban-driven changes in phenotypic variation will have immense implications for urban populations and communities, particularly through urbanisation's effects on individual fitness, species interactions, and conservation. We call here for studies that incorporate phenotypic variation in urban eco-evolutionary research alongside advances in theory.

Urban phenotypic variation

As **urbanisation** (see Glossary) around the world has continued to grow over time, so too have the fields of urban ecology and evolution. Numerous studies have now examined ecological and evolutionary questions across taxa that occupy urban habitats [1–3]. Urban organisms differ from their nonurban conspecifics in many characteristics, and diverse examples show how urbanization affects the mean phenotypes of populations [4]. However, we still know little about how urbanization shapes **phenotypic variation**, the target of **selection** that will determine the ecology and future evolution of urban populations. Few studies have compared phenotypic variation between urban and nonurban populations [5–15] (Table S1 in the supplemental information online) and, to our knowledge, no studies have directly examined the causal mechanisms and consequences of this variation.

Here, we provide an overview of the mechanisms that shape phenotypic variation in urban systems and synthesise potential implications of this variation (Figure 1). Our review focuses on **intraspecific phenotypic variation** between urban and nonurban populations, while emphasising the value in examining phenotypic variation among urban subpopulations within cities alongside **environmental heterogeneity** (Box 1). We discuss sampling considerations (Box 2) and show how urbanisation increases phenotypic variation in an illustrative analysis (Box 3). We note throughout where knowledge is still lacking and recommend future research directions.

Mechanisms shaping phenotypic variation in urban environments

The eco-evolutionary processes that shape the expression of phenotypic variation, and thus diversity, in natural populations have been well studied in a variety of systems [16]. We therefore only provide a brief overview on how different processes such as dispersal, selection, plasticity, and (epi)genetic mutations may shape phenotypic variation in an urban context (overview in Figure 1). We do not provide a general rule for how different processes affect phenotypic variation

Highlights

Phenotypic variation is a neglected phenotypic dimension that could provide valuable biological insights in urban research.

Our synthesis suggests that urbanisation modifies key processes that shape intraspecific variation and may increase phenotypic variation in several urban systems.

We show how urbanisation increases phenotypic variation in an example using tit species across European cities.

Efforts that examine phenotypic variation alongside means in urban research will make valuable contributions towards determing the ecological and evolutionary implications of urban-modified phenotypic variation.

[1]Département des sciences biologiques, Université du Québec à Montréal, 141 Avenue du Président-Kennedy, Montréal, QC H2X 1Y4, Canada
[2]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[3]Institute of Biodiversity, Animal Health & Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, UK
[4]https://www.davidedominoni.com/
[5]https://annecharmantier.weebly.com/

*Correspondence:
thompsonjoymegan@gmail.com
(M.J. Thompson).
@Twitter: @megjoy_(M.J. Thompson),
@p_capi (P. Capilla-Lasheras),
@dmdominoni (D.M. Dominoni),
@DenisREALE (D. Réale) and
@AnneCharmantier (A. Charmantier).

in urban environments as many factors likely contribute to variation in diverse and interactive ways. Overall, however, our synthesis suggests that urbanisation has increased phenotypic variation in several urban systems (Box 3, Table S1 in the supplemental information online).

Dispersal

Whether urbanisation increases or decreases phenotypic variation will partially depend both on a species' **dispersal** abilities and on the direction of dispersal (e.g., **source–sink dynamics**). Dispersal has the potential to promote phenotypic variation within populations through the immigration of new individuals, phenotypes, and genotypes [18]. Nonurban populations might act as source populations [2], whereby constant movements of individuals into urban areas from more natural habitats results in higher phenotypic variation in urban populations. For less dispersive species, however, movements can be restricted by **habitat fragmentation** in urban habitats, which could contribute to declines in variation (via reductions in urban population sizes or increased **genetic drift**; Figure 1) [2], especially if new urban subpopulations are formed by **founder effects** [15,19]. As dispersal in urban environments is still not well studied, further work in this area will be conducive.

Selection

Phenotypic variation could be higher in many urban systems if both environmental heterogeneity (Box 1) and **relaxed selection** allow more diverse phenotypes to persist (Figure 1). By favouring adaptive phenotypes that provide a **fitness** advantage, both directional and stabilising selection can deplete phenotypic variation in a population over time, via a reduction of the underlying genetic variance across generations or the selective disappearance of certain individuals within each generation. However, relaxed selection may be more pervasive in cities than previously thought (e.g., [13], including in humans [20]). A recent meta-analysis found that anthropogenic disturbances in nonurban habitats reduce the strength of selection [21]. On closer examination, the authors found that absolute fitness has increased and variation in fitness decreased because of human disturbance, thus weakening the opportunity for selection. Relaxed selection in urban environments may result from reduced predation pressures, access to supplementary food [22], or a loss of fitness variation [13,21]. Novel and strong selection pressures might affect some urban populations [2,23], but phenotypic variation could still increase in these populations if selection pressures vary with heterogeneity in cities (Box 1). A future focus on phenotypic variation and selection (direction and strength) in and outside cities should provide new biological insights into the processes that affect urban phenotypes and adaptation. These efforts will be especially meaningful as selection is still rarely estimated in urbanised species [2].

Plasticity

Phenotypic plasticity (including **developmental plasticity**) promotes variation and diversification within and between populations [24,25], and may be one of the most common mechanisms allowing individuals to colonise and persist in urban environments [26]. Plasticity could reduce phenotypic variation in an urban population if most individuals are capable of plastic shifts resulting in similar phenotypic expression (Figure 1). A well-studied urban trait that demonstrates this trend is flight initiation distance (FID); the distance an individual allows before retreating when approached by a risky stimulus. Most urban animals would similarly reduce their phenotypic mean, and thus variation, in FIDs if they can adjust their behaviours by habituating to nonthreatening stimuli like humans (via repeated exposures) [27], while nonurban individuals display more variable responses (shown in blue-tailed skinks, *Emoia impar*) [12]. Similarly, a recent meta-analysis shows declines in variation of antipredator behaviours following contact with humans in domesticated, captive, and urban animals [28].

Glossary

Developmental canalisation: a developmental process that constrains phenotypic variation by buffering variation from genetic and/or environmental sources.

Developmental plasticity: the capacity of a genotype to alter its phenotype depending on environmental conditions during ontogeny.

Dispersal: the movement of individuals between geographical areas or habitats.

Environmental heterogeneity: diversity in the presence and arrangement of biotic and abiotic features over space and time.

Epigenetics: the study of any process that alters gene activity (e.g., gene expression) without changing the DNA sequence. These alterations can be heritable and reversible.

Fitness: the contribution of an individual to the gene pool of the next generation, relative to other individuals within a population. Fitness metrics are quantitative measures associated with survival or reproductive output.

Fluctuating selection: changes in the strength or shape of selection through space or time.

Founder effects: a reduction in genetic variation because a population is established by only a few individuals from an ancestral population.

Functional traits: phenotypic traits of an individual that influence their fitness or performance and can affect ecological processes and functions.

Genetic drift: changes in the frequency of gene variants in a population due to random sampling of individuals.

Genetic mutation: permanent alteration of a DNA sequence that results in a genetic variant that may be passed to future offspring.

Habitat fragmentation: landscape-level process that leads to a habitat becoming discontinued.

Intraspecific phenotypic variation: the measurable or observable phenotypic variation within a species.

Matching-habitat choice: the tendency for individuals to settle in a habitat that improves their fitness according to their phenotype, thereby promoting local adaptation.

Phenotypic differentiation: phenotypic differences between two or more (sub)populations.

Phenotypic plasticity: the capacity of a genotype to express different phenotypes depending on environmental conditions.

Conversely, phenotypic variation in urban populations could be higher than nonurban populations because of impaired development and developmental plasticity (Figure 1). Developmental processes act to constrain phenotypic variation among and within individuals (e.g., **developmental canalisation**; [29]), and can be disrupted if the level of an environmental stressor passes a threshold [30]. A recent meta-analysis found that developmental stress decreases the mean, but increases the variation, in diverse phenotypic traits across several taxa [31]. Urban environments may increase variation in populations if the many environmental stressors in these habitats (e.g., noise, light pollution, chemicals, or increased temperature) disrupt developmental processes (Figure 1). For example, impaired head shape development and higher phenotypic variation across head shape indices was found in urban common wall lizards (*Podarcis muralis*) [10]. Early life experiences or environments (e.g., competition, diet, and predation) contribute to phenotypic variation within populations [32,33], but this is not well examined in an urban context.

Mutation and epigenetics

Pollution and environmental stress can increase rates of **genetic mutation**, hypermethylation, or other epigenetic marks [34–37] suggesting that phenotypic variation could increase in urban populations where these processes are occurring at higher rates (Figure 1, Box 3) [38–40]. **Epigenetics** may be an important mechanism of adaptation for urban populations as it can move phenotypes closer to the fitness optimum and increase mutation rates [41], but the role of (epi)genetic mutations in shaping urban phenotypic variation remains unexplored.

Implications of urban phenotypic variation

As shown previously, urban conditions can significantly impact phenotypic variation. These changes in phenotypic variation can have important implications for urban populations, communities, and ecosystems, as well as for conservation programs (Figure 1).

Implications for species interactions, communities, and ecosystem processes

Species abundances and compositions are strongly modified during urbanisation [3,42,43]. Although largely ignored, intraspecific phenotypic variation and its effects on competition [44,45] may have important implications for urban community compositions [46,47]. High trait variation associated with niche expansion can reduce interspecific competition [44,48], potentially to a greater extent in urban environments where individuals adopt novel resources and widen their niches [9,49,50]. Theory also predicts that higher trait variation associated with competitive ability or niche differentiation can lead to the exclusion of competitively inferior species [51]. If increases in intraspecific phenotypic variation in urban exploiters or adapters contributes to competitive exclusions and declines in species richness [50,52], we could see a parallel loss in unique **functional traits** in urban communities that contribute to ecosystem services and functioning [53,54]. For these reasons, invasive species research would benefit from approaches that consider phenotypic variation, particularly in an urban context where native species are confronted with a high frequency of invasions [55,56]. One exemplar study quantified trait variation associated with locomotor performance and temperature tolerance in invasive cane toads (*Rhinella marina*) under laboratory conditions, and then modelled this variation alongside fine-scale climate and landscape data to predict the cane toads fundamental niche and potential for expansion across Australia [57]. Efforts that explore how intraspecific phenotypic variation shapes urban invasions and species compositions would be useful additions to the urban literature, particularly in cases where competitive exclusions disrupt urban ecosystem services [53,58].

Intraspecific phenotypic variation influences trophic interactions that promote ecological processes and services like pollination or seed dispersal [53,59–61]. Wild urban bees, for example,

Phenotypic variation: the measurable or observable variation in a trait.
Relaxed selection: reduction in the strength of the association between fitness and a given phenotype.
Selection: the relationship between fitness and a phenotypic trait. Directional or stabilising selection can decrease phenotypic variation while divergent or disruptive selection can increase phenotypic variation within a population.
Source–sink dynamics: a model that links variation in habitat quality to population dynamics where population growth is expected in high quality or source habitats and population declines are expected in low quality or sink habitats.
Species interactions: interactions between individuals of different species which broadly include interspecific competition, predation, herbivory, parasitism, mutualism, and commensalism.
Urbanisation: a process of environmental change resulting from dense human presence and occupancy.
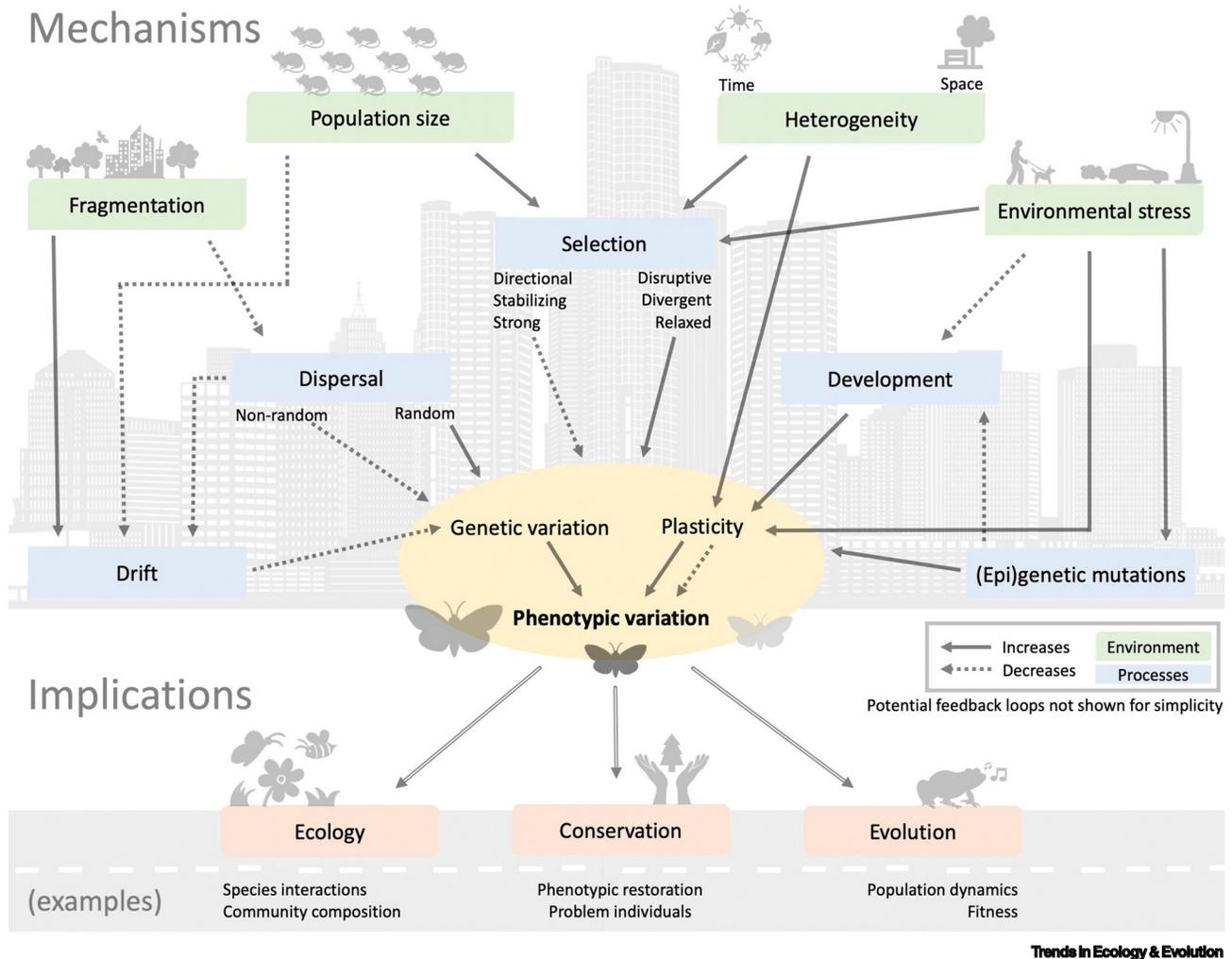
Figure 1. Hypothesised mechanisms that affect intraspecific phenotypic variation within an urban population, and examples of ecological, evolutionary, and conservation management implications of this variation.

have higher intraspecific variation in functional foraging traits than nonurban bees, which may be driven by introductions of non-native and diverse floral resources in urban gardens and parks [6]. Such higher phenotypic variation within species of urban bees might widen their foraging niche and reduce the amount of interactions they have with native flower species (i.e., decreased interaction strength [44,62]). This would have cascading impacts on pollination and, thus, urban plant community composition. Multispecies approaches are needed to explore eco-evolutionary and community dynamics [44,63], but these approaches are still rare in urban research. We recommend future studies quantify and associate phenotypic variation in multiple species to address the consequences of intraspecific phenotypic variation on urban species interactions that are modified along urban gradients.

Urban species interactions can be modified or disrupted if the timing of key life cycle events (i.e., phenology) change, yet considering the role of phenotypic variation in these phenological mismatches has been overlooked so far. Urbanisation has been shown to affect both the peak and duration (i.e., variation) of many phenological events [64] and, sometimes, urbanisation can

Box 1. Environmental heterogeneity and within-city comparisons

Urbanisation could affect intraspecific phenotypic variation differently across subpopulations within a city, and these differences might be in part explained by variable contributions from environmental heterogeneity. Environmental heterogeneity likely plays a large role in urban evolution where interactions between natural and anthropogenic features affect processes such as selection and dispersal [23]. For example, higher environmental heterogeneity within cities compared to natural habitats expose organisms to diverse local conditions that vary in space and time and can contribute to higher phenotypic variation at the city level if trait data are pooled across field sites within the city or across years [8]. **Fluctuating selection** or differential plasticity in response to heterogeneity may also explain why urban subpopulations of common ragweed (*Ambroisa artemisiifolia*) [5] and easter water dragons (*Intellagama lesueurii*) [15] have higher **phenotypic differentiation** than nonurban subpopulations; a pattern shown in a variety of systems at the genetic level [91].

Dispersal could also influence how phenotypic variation is quantified over space if individuals choose environments that best match their phenotype (i.e., **matching-habitat choice**) [92]. Although this is still an unexplored idea in the urban context, there is evidence for habitat matching in urban swans [93] and grasshoppers [94]. Nonrandom dispersal could reduce phenotypic variation within urban subpopulations if like individuals settle in similar urban habitat types, but increase city-level phenotypic variation and differentiation among urban subpopulations (see Figure 1 in main text). Within-city comparisons are needed alongside urban versus nonurban comparisons to disentangle the complex interactions that exist between urban phenotypic variation and heterogeneity at different scales [95,96].

There remains no consensus on whether urban habitats are more environmentally heterogenous, and this is likely because scale is an important, but overlooked factor [46,97]. Urban habitats are known as more spatially heterogenous [98], but less temporally variable [99]. In Table I (extended version in Table S2 in the supplemental information online), we provide examples from the literature that illustrate how urban environmental features may increase or decrease environmental heterogeneity depending on the spatial or temporal scale in consideration. Due to these discrepancies, it will be important for urban studies to report local scale environmental data alongside phenotypic data, so that future work can begin to account for the role of urban heterogeneity at multiple scales.

Table I. Examples demonstrating how environmental features can increase or decrease environmental heterogeneity in urban habitats depending on the scale considered.

Environmental feature	↑ Heterogeneity vs ↓ *heterogeneity*	Scale		Refs
		Spatial[a]	Temporal[b]	
Anthropogenic food sources	Anthropogenic food availability fluctuates over a week.	Small	Short	[100]
	Anthropogenic food sources are more predictable and stable over seasons or years.		Long	[101]
Land cover and vegetation	Land cover fragmentation in urban areas increases spatial heterogeneity.	Small, Large	Long	[98]
	Urban trees have lower species and genetic diversity.	Large		[54,87]
	Higher primary productivity in urban areas, which is more seasonally and annually stable.		Long	[43]
	Local land cover types increase vegetative growing seasons in urban areas.	Small	Long	[102]

See also Table S2 in the supplemental information online for more examples.
[a]Environmental heterogeneity affected at small (local or home range level) or large (city or regional level) spatial scales.
[b]Environmental heterogeneity affected at short (within a day or week) or long (between seasons or years) temporal scales.

cause asynchronous phenological shifts in interacting species. For example, urban plant species tend to flower earlier, but urban pollinators may not show a similar advance in diapause emergence and, thus, their foraging activities can overlap less with key flowering resources [65]. As well, caterpillar emergence in urban environments is more variable and has several small peaks instead of a single peak typical in natural forest habitats [66]. This could have consequences for urban insectivorous birds such as great tits (*Parus major*) who rely on caterpillar prey during nestling provisioning. Urban-modified phenological variation could cause mismatches between interacting species on multiple trophic levels, which would have run-off implications for selection and population dynamics [67].

Box 2. Sampling considerations

As phenotypic variation is a population attribute, it will be important for authors to define what they mean by population when comparing phenotypic variation. A population is often defined in relation to gene flow and drift, but directly calculating population size in many wild species is not feasible [103]. We use the term population loosely in this review to refer to groups of urban and nonurban samples that are spatially close to one another (e.g., individuals in a city vs surrounding area). The type of measurement, size of geographic range, and conspecific density are important sampling factors that could directly affect the amount of phenotypic variation estimated in a population. Therefore, the scale considered (see also Box 1) and the sampling design used might affect the amount of phenotypic variation measured, particularly in cross-sectional studies. Comparing variation between two samples requires standardized measures of variation (e.g., coefficient of variation) that consider the scale of the trait measured and the mean–standard deviation relationship (further discussion in [104]).

Many studies, including meta-analyses [21], focus on comparing two contrasting populations, one urban and one nonurban. This may create biases in comparative analyses or review syntheses if the definition of urban and nonurban sites differs between studies. For instance, sites that are defined as urban can differ in size or location within a city. Small green areas in city centres, and large parks or cemeteries, can equally be considered as urban, but they are likely to be different ecologically. Sometimes, the urban environment is sampled in a more heterogenous way than in more classic urban studies, which includes randomly selecting sampling locations [105] or using hierarchical designs [95]. It is worth noting that such alternative designs could lead to larger phenotypic variation in the urban population, because they are likely to sample a larger array of microhabitats.

We wish to both point out these sampling considerations and acknowledge that dealing with these issues uniformly across studies in free-ranging populations can be challenging. We recommend researchers control for unbalanced sampling and report relevant information about their study populations when comparing phenotypic variation, for instance by explicitly quantifying the level of urbanization at study sites. Urbanization or urban environmental features are still not well quantified in many studies that examine phenotypic shifts. In particular, environmental measures are often anthropomorphically biased and may not represent the environmental scales that urban organisms occupy [106].

Implications for fitness, selection, and population dynamics

Intraspecific phenotypic variation can also influence population dynamics [68–70]. For example, higher intraspecific trait variation can promote diverse individual responses to environmental fluctuations that buffer and stabilise population dynamics (i.e., portfolio effects) [44]; a process that is especially applicable to urban populations undergoing rapid environmental change [46,71]. Phenotypic variation can also drive population dynamics through selection [68,72], particularly during colonisation events [73]. Therefore, we anticipate that *a priori* knowledge on how phenotypic variation influences fitness or performance metrics will be useful when exploring urban selection and population implications.

Variation among individuals in their sexual signals can alter reproductive behaviours and selection in urban populations. Higher variation in mate qualities can increase the benefits of choosiness, mate searching behaviours, and intrasexual competition. These dynamics may be especially relevant in urban environments where pollution (e.g., chemical, nutrient, noise, and light) can disrupt the communication and mating behaviours of animals [74,75]. For example, several species experience increased access to key nutrients in urban environments that can reduce individual variation in the honesty of sexual signals that indicate an individual's ability to acquire resources [74]. Mate choice can also be affected by urban pollution or stressors which can reduce the perceived variation in sexual signals. For instance, the visual mating signals of three-spined stickle-backs (*Gasterosteus aculeatus*) have been disrupted by human-induced algal blooms. As a result, females are unable to perceive variation among males in their sexual signals and are, thus, more likely to choose lower quality mates that produce less viable offspring [76]. Maladaptive mating in urban habitats could impede adaptation, contribute to population declines, or divergences in mean phenotypes, potentially resulting in hybridisation or speciation [75,77].

Modified natural selection in urban environments could also alter phenotypic variation, potentially resulting in life-history trade-offs or changes in subsequent selective processes. Urban Túngara

Box 3. Morphological variation in urban versus forest tits

We conducted an illustrative analysis to examine how urbanisation may affect phenotypic variation of morphological traits using data on great and blue tits (*Parus major* and *Cyanistes caeruleus*) from a collaborative network of researchers across 13 different European forest and city pairs (Figure I, and Table S3, Figures S1 and S2 in the supplemental information online). First, we expected urbanisation to decrease the mean of morphological traits based on previous findings [107,108]. Second, we hypothesised an increase in phenotypic variation for morphology in urban tits because (i) environmental stress can increase (epi)genetic mutations or disrupt developmental mechanisms; (ii) fluctuating selection pressures via environmental heterogeneity might increase morphological variation within urban tit populations; and (iii) European tits are good dispersers [109], which should reduce the effects of fragmentation that act to decrease phenotypic variation in urban populations for other less-dispersive taxa. We used lnRR (ln $\frac{Mean_{urban}}{Mean_{nonurban}}$) and lnCVR ($\approx$ ln $\frac{CV_{urban}}{CV_{nonurban}}$) to compare morphological mean and variance, respectively, between urban and nonurban tits from multiple systems (see supplementary information online for details) [110].

Urbanisation tended to decrease the mean (lnRR), but increase the variation (lnCVR), in morphology as predicted. Urban birds tended to be smaller, with this effect being stronger in mass and tarsus length than wing length (Figure I, Table S4 in the supplemental information online). Tits tended to have more variable body sizes in cities, a trend driven mainly by tarsus length (Figure I, Table S4 in the supplemental information online). Estimates of mean and variance effect sizes were similar for the two species, and slightly stronger in females than males (Figure S3 and Table S4 in the supplemental information online). Multiple of the above hypotheses may explain this increased morphological variation in urban tits. For example, the morphological traits we examine have different developmental trajectories where the tarsus develops early in life and remains fixed, wing metrics can vary annually with moults, and body mass can fluctuate continuously. Disruptions in development could then only have observable effects on variation for early developing and nonlabile traits, like tarsus length. Fluctuating selection and high heterogeneity among urban habitats could also increase morphological variation in tits at the city level (Box 1). This analysis reveals that urbanisation increases phenotypic variation in tit morphology. Further work is needed to determine the mechanisms that interact to affect shifts in phenotypic variation in urban environments, as well as the consequences of higher phenotypic variation in cities.
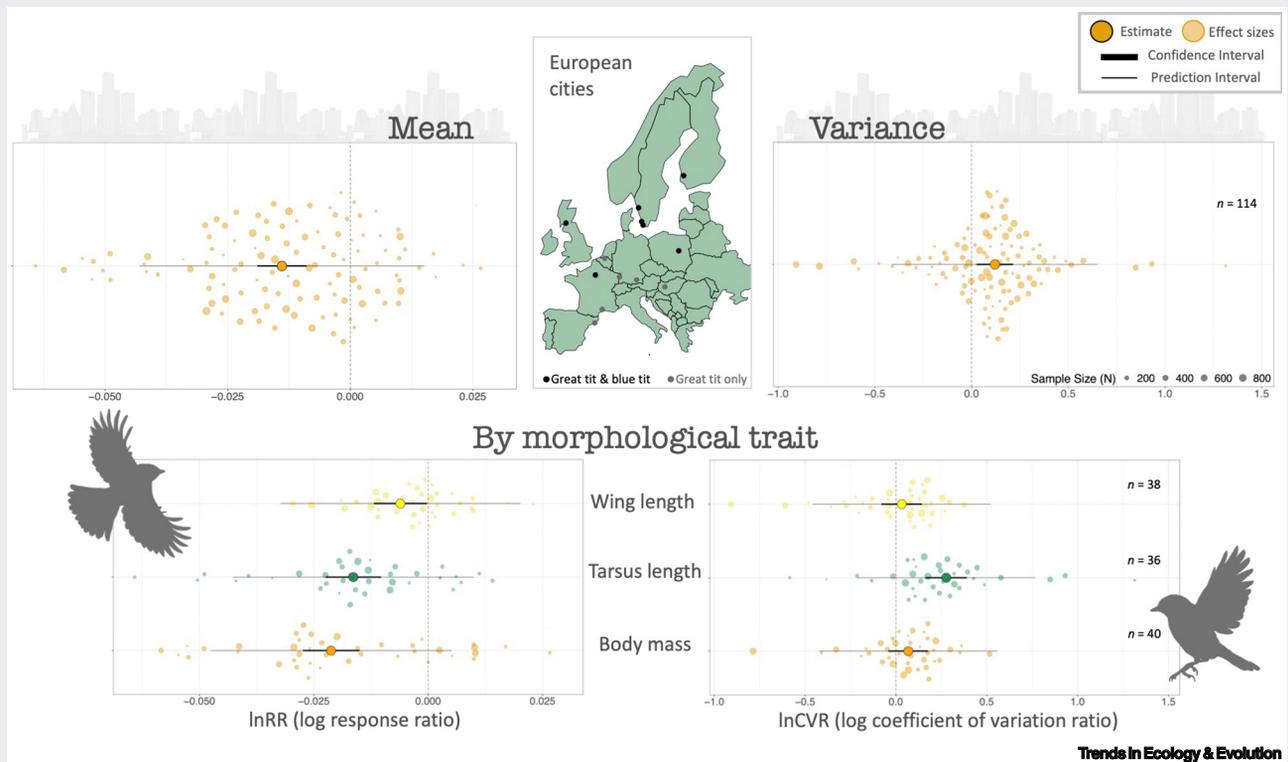

Figure I. Urbanisation increases the variance (lnCVR; right), but decreases the mean (lnRR; left), in European tit morphology. Models evaluating the overall effect of urbanisation (top) and contributions from morphological traits (bottom) are shown. Individual effect sizes (*n* = 114) are shown and scaled by their sample size. See also Tables S3 and S4, and Figures S1–S3 in the supplemental information online for detailed information and results.

frogs (*Physalaemus pustulosus*), for example, experience reduced predation and parasitism risk while singing (relaxed natural selection) and higher competition for mates (stronger sexual selection) [78]. As a result, urban frogs call at higher rates, sing more complex and attractive songs, and plastically adjust their songs to sound and light levels in the environment. The authors

suggest that a broader range of sexual signalling in urban frogs (i.e., higher phenotypic variation) afford them reproductive and survival advantages over the more natural forest phenotype [78]. Phenotypic changes via plasticity can increase fitness and promote adaptation in novel or stressful environments, but plasticity likely incurs significant costs, for example by reducing growth rates, generation times, or fecundity [79]. Thus, populations that show adaptive plastic responses or higher phenotypic variation in response to novel environments could also shift toward slower life histories [79]. As many urban phenotypic changes may involve plasticity [26], including the example in Túngara frogs, it would be interesting to explore the role of urban-modified phenotypic variation in life-history trade-offs and pace of life [80,81]. The selective and demographic consequences of urban-modified life history variation are unexplored in most urban systems, hence efforts tackling these ideas will provide timely insights into how sexual and natural selection shape urban populations.

Beyond quantifying phenotypic variation in urban populations, urban studies should also aim to determine to what extent a phenotypic trait is heritable [82]. This is especially important if the adaptive or evolutionary implications of urban phenotypic variation are to be explored. While intraspecific phenotypic variation has a key role in influencing urban eco-evolutionary dynamics, it is highly informative to decipher between its genetic and environmental origins, and their inter-actions [63,83]. Exploring the origins of urban phenotypic variation calls on quantitative genetic approaches using long-term data or experimental approaches like common gardens [4]. Fear of humans, for example, is commonly thought to decrease in urban animals via habituation to humans, a form of phenotypic plasticity. However, variation in behavioural responses to humans is more heritable than expected in urban burrowing owls (*Athene cunicularia*), suggesting that a reduced fear of humans could also result from an evolutionary response [84]. Efforts making these distinctions are not commonly applied as large datasets or intensive experiments are required, but we emphasize here the value of these efforts in urban research.

Implications for urban conservation management
The advantages of incorporating intraspecific variation into urban conservation management has been highlighted recently [71,85]. Increasing phenotypic variation in populations of conservation concern has been suggested as an effective management approach in urban contexts. For example, phenotypic restoration initiatives can help establish lost phenotypic variation through reintroductions of missing phenotypes. Simulations have shown how reintroductions of larger seed types in human-impacted forests can help restore seed profiles back to natural levels and maintain seed dispersal [60]. Efforts that increase phenological variation by extending the duration of key events in particular species, like flowering time, might help interacting species, like specialist pollinators, that experience asynchronous shifts due to environmental change [86]. Promoting trait diversity through management programs has also been recognised in urban arboriculture where urban forests tend to consist of similar species [54] or clones [87]. Low phenotypic variation among planted urban trees increases vulnerability to drought or pests and can hamper the ecosystem services provided by trees in cities, and so increasing trait diversity in trees can offer an easy urban management approach to counter these challenges [54]. Trait distributions likely have very different implications for population growth and stability than trait means, and so including intraspecific phenotypic variation in population monitoring is warranted [45].

Phenotypic variation can also be used as a tool to regulate urban populations that cause prob-lems for native species and humans. Selective management approaches, for instance, decrease phenotypic variation within a population by targeting 'problem individuals' that possess certain phenotypes associated with human impacts and conflicts [88]. For example, efforts evaluating personality variation in deer populations show that deer with bolder personalities may be more

likely to cause human harm through vehicle collisions, crop damage, or disease transmission [89]. Simulations suggest that selective harvesting of deer with bolder personality types could mitigate human–wildlife conflicts while sustaining population sizes [89]. These management programmes would be especially useful in urban environments at the human–wildlife interface, but they require some knowledge of the phenotypic variation contained within target populations. We expect that studies exploring the implications of phenotypic variation in human–wildlife conflicts will help ensure that management interventions are successful and have longer lasting impacts [88].

Conservation programmes could aim to increase intraspecific variation in populations they want to conserve and decrease variation in populations they want to mitigate [58,85]. This is because higher intraspecific variation should have positive ecological effects on populations, in particular when the population mean traits are not well matched to the fitness optimum of the environment (i.e., phenotype–environment mismatch) [69], which might be more frequently observed in urban populations. However, increasing phenotypic variation will not always benefit populations if individuals are already well adapted to environmental conditions. A theoretical study demonstrates this and shows that high amounts of phenotypic variation will have increasingly negative ecological consequences on populations as they become better adapted to the local environmental optimum [90]. It will be imperative for urban monitoring programmes to evaluate how variation and means associate with local fitness optima to better anticipate the implications of efforts that manage variation [69,85]. We suggest that these evaluations occur on fine scales as phenotype–environment mismatches may differ substantially among urban subpopulations due to within-city heterogeneity (Box 1). Considering phenotypic variation in urban conservation has great promise and city municipalities could benefit from more focused research in this area. We, however, recommend caution and prior investigations to comprehend the possible ecological and evolutionary implications of such interventions.

Concluding remarks

Our synthesis suggests that urban conditions impact phenotypic variation through various processes, and that urban effects on phenotypic variation have ecological, evolutionary, and management implications. We expect phenotypic variation to increase in urban systems through dispersal, relaxed or heterogenous selection, developmental plasticity, (epi)genetic mutations, or a combination of these (Figure 1, Boxes 1 and 3, Table S1 in the supplemental information online). The synergistic and counteractive effects of these mechanisms could shape variation in diverse and complex ways, and care will need to be taken to ensure appropriate sampling design in urban studies (Box 2). Urbanisation has significant impacts on species interactions and individual fitness, which may exaggerate the effects of intraspecific phenotypic variation in urban systems. Examining these hypotheses across cities, taxa, and traits will be important for further generalizing how urbanisation affects phenotypic variation, and in turn how variation affects evolutionary and environmental change.

Most urban ecology/evolution projects already have data on the variance around phenotypes in their study populations and we, therefore, hope to encourage the comparison of variation, beside means, of ecologically relevant traits in future work [31]. To this end, we show in a preliminary analysis that urbanisation increases the variation in morphological traits in tit species across Europe (Box 3). There is a need to examine phenotypic variation both between and within cities (Box 1), and to examine contributions of environmental heterogeneity on phenotypic variation at spatial and temporal scales relevant to a species' biology (Box 2; see also Outstanding questions).

Outstanding questions

Are trends in phenotypic variation consistent across cities?

How does phenotypic variation correlate with environmental heterogeneity within cities?

Are trends in urban phenotypic variation consistent across diverse traits? Are mechanisms differentially shaping variation of different types of traits?

The type of urban and nonurban habitats selected may affect whether urban and nonurban groups are found to differ in their phenotypic variation (Box 2). How does sampling design affect the amount of variation quantified?

In which urban organisms should we expect increases or decreases in phenotypic variation? Is the dispersal ability of an organism a main determinant for whether we see increases in urban phenotypic variation?

Does nonrandom dispersal contribute to lower phenotypic variation locally, but higher variation within heterogeneous cities?

If semiurban habitats or green spaces within cities represent isolated patches with unique environmental conditions for some species, could we expect nonlinear relationships between the degree of urbanisation and phenotypic variation?

How does the direction and strength of selection shape phenotypic variation in urban systems, and does this affect subsequent evolution?

Which developmental conditions or environmental drivers modify phenotypic variation within urban habitats compared to natural habitats?

Which role, if any, do (epi)genetic mutations play in shaping urban phenotypic variation and how do these mutations associate with fitness?

Do differences in phenotypic variation between urban and nonurban populations have implications for conservation of biodiversity in cities?

efforts and comradery. MJT is supported by a Canadian Graduate Scholarship from the Natural Sciences and Engineering Research Council (NSERC) of Canada and a PhD mobility grant from le Centre Méditerranéen de l'Environnement et de la Biodiversité (CeMEB). This project was funded by the Agence Nationale de la Recherche (URBANTIT grant ANR-19-CE34-0008-05 to AC) and a Fonds de Recherche du Quebec Nature et Technologie to DR. Artwork in figures were created by MJT aside from the city skyline which was obtained under a creative commons license.

Declaration of interests

No interests are declared.

Supplemental Information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2021.09.009.

Can cities serve as reservoirs of (phenotypic) variation that may facilitate potential adaptation in a scenario of global change?

How does intraspecific phenotypic variation modify species interactions and ecological processes? In which instances would phenotypic management approaches be most effective in urban conservation?

References

1. Szulkin, M. *et al.* (2020) *Urban Evolutionary Biology*, Oxford University Press
2. Johnson, M.T.J. and Munshi-South, J. (2017) Evolution of life in urban environments. *Science* 358, 1–11
3. Diamond, S.E. and Martin, R.A. (2021) Evolution in cities. *Annu. Rev. Ecol. Evol. Syst.* 52, 519–540
4. Lambert, M.R. *et al.* (2021) Adaptive evolution in cities: progress and misconceptions. *Trends Ecol. Evol.* 36, 239–257
5. Gorton, A.J. *et al.* (2018) Little plant, big city: a test of adaptation to urban environments in common ragweed (*Ambrosia artemisiifolia*). *Proc. R. Soc. B Biol. Sci.* 285, 20180968
6. Eggenberger, H. *et al.* (2019) Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *J. Anim. Ecol.* 88, 1522–1533
7. Theodorou, P. *et al.* (2021) Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. *Evol. Appl.* 14, 53–68
8. Multini, L.C. *et al.* (2019) Urbanization as a driver for temporal wing-shape variation in *Anopheles cruzii* (Diptera: Culicidae). *Acta Trop.* 190, 30–36
9. Falvey, C.H. *et al.* (2020) The finer points of urban adaptation: intraspecific variation in lizard claw morphology. *Biol. J. Linn. Soc.* 131, 304–318
10. Lazić, M.M. *et al.* (2015) Effects of environmental disturbance on phenotypic variation: an integrated assessment of canalization, developmental stability, modularity, and allometry in lizard head shape. *Am. Nat.* 185, 44–58
11. Gómez-Benitez, A. *et al.* (2021) The influence of urbanization on morphological traits in the Balsas Basin Whiptail lizard (*Aspidoscelis costatus costatus*). *Urban Ecosyst.* 24, 327–333
12. Williams, D.M. *et al.* (2019) High human disturbance decreases individual variability in skink escape behavior. *Curr. Zool.* 66, 63–70
13. Rodewald, A.D. and Arcese, P. (2017) Reproductive contributions of cardinals are consistent with a hypothesis of relaxed selection in urban landscapes. *Front. Ecol. Evol.* 5, 1–7
14. Bókony, V. *et al.* (2012) Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS One* 7, e36639
15. Littleford-Colquhoun, B.L. *et al.* (2017) Archipelagos of the Anthropocene: rapid and extensive differentiation of native terrestrial vertebrates in a single metropolis. *Mol. Ecol.* 26, 2466–2481
16. Mitchell-Olds, T. *et al.* (2007) Which evolutionary processes influence natural genetic variation for phenotypic traits? *Nat. Rev.* 8, 845–856
17. Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends Ecol. Evol.* 17, 183–189
18. Mueller, J.C. *et al.* (2018) Evolution of genomic variation in the burrowing owl in response to recent colonization of urban areas. *Proc. R. Soc. B Biol. Sci.* 285, 20180206
19. You, W. and Henneberg, M. (2018) Relaxed natural selection contributes to global obesity increase more in males than in females due to more environmental modifications in female body mass. *PLoS One* 13, 1–20

20. Fugère, V. and Hendry, A.P. (2018) Human influences on the strength of phenotypic selection. *Proc. Natl. Acad. Sci. U. S. A.* 115, 10070–10075
21. Lahti, D.C. *et al.* (2009) Relaxed selection in the wild. *Trends Ecol. Evol.* 24, 487–496
22. Rivkin, L.R. *et al.* (2019) A roadmap for urban evolutionary ecology. *Evol. Appl.* 12, 384–398
23. Pfennig, D.W. *et al.* (2010) Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* 25, 459–467
24. Gilbert, S.F. *et al.* (2015) Eco-Evo-Devo: developmental symbiosis and developmental plasticity as evolutionary agents. *Nat. Rev. Genet.* 16, 611–622
25. Hendry, A.P. *et al.* (2008) Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* 17, 20–29
26. Blumstein, D.T. (2016) Habituation and sensitization: new thoughts about old ideas. *Anim. Behav.* 120, 255–262
27. Geffroy, B. *et al.* (2020) Evolutionary dynamics in the anthropocene: life history and intensity of human contact shape antipredator responses. *PLoS Biol.* 18, e3000818
28. Willmore, K.E. *et al.* (2007) Phenotypic variability: Its components, measurement and underlying developmental processes. *Evol. Biol.* 34, 99–120
29. Hoffman, A.A. and Hercus, M.J. (2000) Environmental stress as an evolutionary force. *Bioscience* 50, 217–226
30. Sánchez-Tójar, A. *et al.* (2020) Illustrating the importance of meta-analysing variances alongside means in ecology and evolution. *J. Evol. Biol.* 33, 1216–1223
31. Nicolaus, M. *et al.* (2016) Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecol. Lett.* 19, 478–486
32. Dirienzo, N. *et al.* (2019) Juvenile social experience generates differences in behavioral variation but not averages. *Behav. Ecol.* 30, 455–464
33. Yauk, C. *et al.* (2008) Germ-line mutations, DNA damage, and global hypermethylation in mice exposed to particulate air pollution in an urban/industrial location. *Proc. Natl. Acad. Sci. U. S. A.* 105, 605–610
34. Somers, C.M. *et al.* (2004) Reduction of particulate air pollution lowers the risk of heritable mutations in mice. *Science.* 304, 1008–1010
35. Eeva, T. *et al.* (2006) Environmental pollution affects genetic diversity in wild bird populations. *Mutat. Res.* 608, 8–15
36. Yauk, C.L. *et al.* (2000) Induced minisatellite germline mutations in herring gulls (*Larus argentatus*) living near steel mills. *Mutat. Res. Fundam. Mol. Mech. Mutagen.* 452, 211–218
37. Watson, H. *et al.* (2020) Urbanisation is associated with modifications in DNA methylation in a small passerine bird. *Evol. Appl.* 14, 85–98
38. Riyahi, S. *et al.* (2015) Combined epigenetic and intraspecific variation of the DRD4 and SERT genes influence novelty seeking behavior in great tit *Parus major*. *Epigenetics* 10, 516–525
39. McNew, S.M. *et al.* (2017) Epigenetic variation between urban and rural populations of Darwin's finches. *BMC Evol. Biol.* 17, 1–14

40. Perrier, C. *et al.* (2020) Adaptation genomics in urban environments. In *Urban Evolutionary Biology* (Szulkin, M. *et al.*, eds), pp. 74–90, Oxford University Press

41. Marques, P.S. *et al.* (2019) Intraspecific trait variation in urban stream ecosystems: toward understanding the mechanisms shaping urban stream communities. *Freshw. Sci.* 38, 1–11

42. Faeth, S.H. *et al.* (2005) Trophic dynamics in urban communities. *Bioscience* 55, 399–407

43. Bolnick, D.I. *et al.* (2011) Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192

44. Moran, E.V. *et al.* (2016) Intraspecific trait variation across scales: implications for understanding global change responses. *Glob. Chang. Biol.* 22, 137–150

45. Alberti, M. *et al.* (2020) The complexity of urban eco-evolutionary dynamics. *Bioscience* 70, 772–793

46. Des Roches, S. *et al.* (2018) The ecological importance of intraspecific variation. *Nat. Ecol. Evol.* 2, 57–64

47. Violle, C. *et al.* (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27, 244–252

48. Pagani-Núñez, E. *et al.* (2019) Niches in the anthropocene: passerine assemblages show niche expansion from natural to urban habitats. *Ecography* 42, 1360–1369

49. De León, L.F. *et al.* (2019) Urbanization erodes niche segregation in Darwin's finches. *Evol. Appl.* 12, 1329–1343

50. Hart, S.P. *et al.* (2016) How variation between individuals affects species coexistence. *Ecol. Lett.* 19, 825–838

51. Barabás, G. and D'Andrea, R. (2016) The effect of intraspecific variation and heritability on community pattern and robustness. *Ecol. Lett.* 19, 977–986

52. Sol, D. *et al.* (2020) The worldwide impact of urbanisation on avian functional diversity. *Ecol. Lett.* 23, 962–972

53. Paquette, A. *et al.* (2021) Praise for diversity: a functional approach to reduce risks in urban forests. *Urban For. Urban Green.* 62, 127157

54. Gaertner, M. *et al.* (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. *Biol. Invasions* 19, 3461–3469

55. Forsman, A. (2014) Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. *Proc. Natl. Acad. Sci. U. S. A.* 111, 302–307

56. Kolbe, J.J. *et al.* (2010) Modeling the consequences of thermal trait variation for the cane toad invasion of Australia. *Ecol. Appl.* 20, 2273–2285

57. Des Roches, S. *et al.* (2021) Conserving intraspecific variation for nature's contributions to people. *Nat. Ecol. Evol.* 5, 574–582

58. Zwolak, R. (2018) How intraspecific variation in seed-dispersing animals matters for plants. *Biol. Rev.* 93, 897–913

59. Carvalho, C. da S. *et al.* (2021) Rescuing intraspecific variation in human-impacted environments. *J. Appl. Ecol.* 58, 350–359

60. Snell, R.S. *et al.* (2019) Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants* 11, 1–19

61. Gibert, J.P. and Brassil, C.E. (2014) Individual phenotypic variation reduces interaction strengths in a consumer-resource system. *Ecol. Evol.* 4, 3703–3713

62. De Meester, L. *et al.* (2019) Analysing eco-evolutionary dynamics – the challenging complexity of the real world. *Funct. Ecol.* 33, 43–59

63. Jochner, S. and Menzel, A. (2015) Urban phenological studies – past, present, future. *Environ. Pollut.* 203, 250–261

64. Fisogni, A. *et al.* (2020) Urbanization drives an early spring for plants but not for pollinators. *Oikos* 129, 1681–1691

65. Pollock, C.J. *et al.* (2017) Integrated behavioural and stable isotope data reveal altered diet linked to low breeding success in urban-dwelling blue tits (*Cyanistes caeruleus*). *Sci. Rep.* 7, 1–14

66. Visser, M.E. and Gienapp, P. (2019) Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* 3, 879–885

67. Pelletier, F. *et al.* (2007) The evolutionary demography of ecological change: linking trait variation and population growth. *Science* 315, 1571–1574

68. Gibert, J.P. (2016) The effect of phenotypic variation on meta-population persistence. *Popul. Ecol.* 58, 345–355

69. Wright, J.P. *et al.* (2016) The more things change, the more they stay the same? When is trait variability important for stability of ecosystem function in a changing environment. *Philos. Trans. R. Soc. B Biol. Sci.* 371, 20150272

70. Mimura, M. *et al.* (2017) Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evol. Appl.* 10, 121–139

71. Farine, D.R. *et al.* (2015) From individuals to groups and back: the evolutionary implications of group phenotypic composition. *Trends Ecol. Evol.* 30, 609–621

72. Duckworth, R.A. and Aguillon, S.M. (2015) Eco-evolutionary dynamics: investigating multiple causal pathways linking changes in behavior, population density and natural selection. *J. Ornithol.* 156, 115–124

73. Snell-Rood, E. *et al.* (2015) Life-history evolution in the anthropocene: effects of increasing nutrients on traits and trade-offs. *Evol. Appl.* 8, 635–649

74. Candolin, U. and Wong, B.B.M. (2019) Mate choice in a polluted world: consequences for individuals, populations and communities. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180055

75. Candolin, U. *et al.* (2016) Environmental change disrupts communication and sexual selection in a stickleback population. *Ecology* 97, 969–979

76. Thompson, K.A. *et al.* (2018) Speciation and the city. *Trends Ecol. Evol.* 33, 815–826

77. Halfwerk, W. *et al.* (2019) Adaptive changes in sexual signalling in response to urbanization. *Nat. Ecol. Evol.* 3, 374–380

78. Snell-Rood, E.C. *et al.* (2018) Mechanisms of plastic rescue in novel environments. *Annu. Rev. Ecol. Evol. Syst.* 49, 331–354

79. Sepp, T. *et al.* (2017) A review of urban impacts on avian life-history evolution: does city living lead to slower pace of life? *Glob. Chang. Biol.* 24, 1452–1469

80. Brans, K.I. and De Meester, L. (2018) City life on fast lanes: urbanization induces an evolutionary shift towards a faster lifestyle in the water flea *Daphnia*. *Funct. Ecol.* 32, 2225–2240

81. Hoffmann, A.A. and Merilä, J. (1999) Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.* 14, 96–101

82. Brans, K.I. *et al.* (2017) Eco-evolutionary dynamics in urbanized landscapes: evolution, species sorting and the change in zooplankton body size along urbanization gradients. *Philos. Trans. R. Soc. B Biol. Sci.* 372, 20160030

83. Carrete, M. *et al.* (2016) Heritability of fear of humans in urban and rural populations of a bird species. *Sci. Rep.* 6, 1–6

84. Lambert, M.R. and Donihue, C.M. (2020) Urban biodiversity management using evolutionary tools. *Nat. Ecol. Evol.* 4, 903–910

85. Olliff-Yang, R.L. *et al.* (2020) Mismatch managed? Phenological phase extension as a strategy to manage phenological asynchrony in plant–animal mutalisms. *Restor. Ecol.* 28, 498–505

86. Vanden Broeck, A. *et al.* (2018) Genetic diversity loss and homogenization in urban trees: the case of *Tilia × europaea* in Belgium and the Netherlands. *Biodivers. Conserv.* 27, 3777–3792

87. Swan, G.J.F. *et al.* (2017) Ecology of problem individuals and the efficacy of selective wildlife management. *Trends Ecol. Evol.* 32, 518–530

88. Honda, T. *et al.* (2018) A review of urban wildlife management from the animal personality perspective: The case of urban deer. *Sci. Total Environ.* 644, 576–582

89. Dibble, C.J. and Rudolf, V.H.W. (2019) Phenotype-environment matching predicts both positive and negative effects of intraspecific variation. *Am. Nat.* 194, 47–58

90. Miles, L.S. *et al.* (2019) Gene flow and genetic drift in urban environments. *Mol. Ecol.* 28, 4138–4151

91. Edelaar, P. and Bolnick, D.I. (2012) Non-random gene flow: an underappreciated force in evolution and ecology. *Trends Ecol. Evol.* 27, 659–665

92. van Dongen, W.F.D. *et al.* (2015) Variation at the DRD4 locus is associated with wariness and local site selection in urban black swans. *BMC Evol. Biol.* 15, 1–11

93. Camacho, C. *et al.* (2020) Experimental evidence that matching habitat choice drives local adaptation in a wild population. *Proc. R. Soc. B Biol. Sci.* 287, 20200721

94. Merckx, T. *et al.* (2018) Body-size shifts in aquatic and terrestrial urban communities. *Nature* 558, 113–116

95. Oliveira Hagen, E. *et al.* (2017) Impacts of urban areas and their characteristics on avian functional diversity. *Front. Ecol. Evol.* 5, 1–15

96. Uchida, K. *et al.* (2021) Urban biodiversity and the importance of scale. *Trends Ecol. Evol.* 36, 123–131

97. Pickett, S.T.A. *et al.* (2017) Dynamic heterogeneity: a framework to promote ecological integration and hypothesis generation in urban systems. *Urban Ecosyst.* 20, 1–14

98. Shochat, E. *et al.* (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* 21, 186–191

99. Stofberg, M. *et al.* (2019) Juggling a "junk-food" diet: responses of an urban bird to fluctuating anthropogenic-food availability. *Urban Ecosyst.* 22, 1019–1026

100. Tryjanowski, P. *et al.* (2015) Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. *Environ. Sci. Pollut. Res.* 22, 15097–15103

101. Qiu, T. *et al.* (2017) Impacts of urbanization on vegetation phenology over the past three decades in Shanghai, China. *Remote Sens.* 9, 1–16

102. Marko, P.B. and Hart, M.W. (2011) The complex analytical landscape of gene flow inference. *Trends Ecol. Evol.* 26, 448–456

103. Pélabon, C. *et al.* (2020) On the use of the coefficient of variation to quantify and compare trait variation. *Evol. Lett.* 4, 180–188

104. Sprau, P. *et al.* (2017) Multidimensional environmental predictors of variation in avian forest and city life histories. *Behav. Ecol.* 28, 59–68

105. Szulkin, M. *et al.* (2020) How to quantify urbanization when testing for urban evolution? In *Urban Evolutionary Biology* (Szulkin, M. *et al.*, eds), pp. 13, Oxford University Press

106. Caizergues, A.E. *et al.* (2021) An avian urban morphotype: how the city environment shapes great tit morphology at different life stages. *Urban Ecosyst.* 24, 929–941

107. Senar, J.C. and Björklund, M. (2021) Recent spread of blue tits into the Barcelona urban environment : morphological differences and the role of balanced dispersal. *Evol. Ecol.* 35, 83–99

108. Salmón, P. *et al.* (2021) Continent-wide genomic signatures of adaptation to urbanisation in a songbird across Europe. *Nat. Commun.* 12, 2983

109. Nakagawa, S. *et al.* (2015) Meta-analysis of variation: ecological and evolutionary applications and beyond. *Methods Ecol. Evol.* 6, 143–152