



## REVIEW

Callow-Grace Review

## How does urbanization affect natural selection?

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## Abstract

1. Urbanization is one of the most significant contributors to the Anthropocene, and urban evolutionary ecology has become an important field of research. While it is commonly assumed that cities impose new and stronger selection, the contradictory assertion that selection may be relaxed in cities is also frequently mentioned, and overall, our understanding of the effects of urbanization on natural selection is incomplete.
2. In this review, we first conduct a literature search to find evidence for patterns of natural selection on phenotypic traits including morphology, physiology, behaviour and life history, in urban and non-urban populations of animals and plants. This search reveals that coefficients of natural selection in the context of urbanization are scarce ( $n=8$  studies providing selection gradients/differentials that include a total of  $n=200$  coefficients) and a lack of standardized methods hinders quantitative comparisons across studies (e.g. with meta-analysis). These studies, however, provide interesting insight on the agents shaping natural selection in cities and improve our mechanistic understanding of selection processes at different spatial scales.
3. We then perform a second literature search to review genomic studies assessing selection intensity in cities, on the genome of non-human natural populations. While this search returns 383 articles, only 34 of these truly investigate footprints of selection associated with urbanization, and only one study provides urban genetic selection coefficients. Here again, we find highly heterogeneous approaches, yet some studies provide strong evidence of genomic footprints of urban adaptation.
4. In neither the phenotypic nor genomic literature review were we able to quantitatively assess natural selection across urban versus non-urban habitats. Thus, we propose a roadmap of how future studies should provide standardized metrics to

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facilitate mega- or meta-analyses and explore generalized effects of urbanization on selection.

#### KEYWORDS

city, evolution, genomic, literature review, natural populations, phenotypic, selection coefficient, Urban adaptation

## 1 | INTRODUCTION

The Anthropocene is defined as the period during which human activity has demonstrably impacted the planet's geology, climate and ecosystems (Waters et al., 2016). The consequences of human impacts on the planet have included rapid shifts in the phenotypes of wild organisms in response to anthropogenic disturbances (Hendry et al., 2008), such as a reduction in the size of harvested (i.e. fished or hunted) animals (Darimont et al., 2009) or the repeated evolution of extreme pollution tolerance in populations of Atlantic killifish (*Fundulus heteroclitus*) of urban estuaries (Whitehead et al., 2012). These human-induced phenotypic shifts are driven by both rapid plasticity and genetic responses (Palumbi, 2001). Pervasive ecological alterations, such as habitat degradation, climate change, pollution, exotic species introduction, or over-exploitation of resources, may in turn influence evolutionary processes such as gene flow, mutation rate, genetic drift and natural selection. The related eco-evolutionary feedback loops impede analysis of these individual processes, and predicting the future eco-evolutionary consequences of the human footprint on biodiversity is challenging (Hendry et al., 2017; Otto, 2018; Pelletier et al., 2007; Wood et al., 2021).

Despite the difficulty in studying these processes independently, there is a general consensus that 'human activities have reshaped selection pressures' (Otto, 2018). Perhaps there is already a general agreement on this statement because of long-standing evidence that humans can intentionally initiate and control artificial selection such as during plant or animal domestication (Driscoll et al., 2009). In fact, from Darwin to modern quantitative genetics, agricultural domestication has resulted in huge steps in our understanding of natural selection and adaptive evolution (e.g. Gregory, 2009; Thompson, 2008). Humans can also unintentionally influence the direction, shape and strength of natural selection. Contrary to the common expectation that human activities will result in novel and strong selection (Pelletier & Coltman, 2018), a review of phenotypic selection coefficients across 37 different species found no evidence for stronger selection on average in human-disturbed compared to natural habitats, with notable exceptions such as strong size-related selection in fisheries (Fugere & Hendry, 2018). Despite these findings, there is still a pervasive assumption in the literature that human altered environments, and in particular urban habitats, are 'a powerful selective force' (Grimm et al., 2008) that can 'increase the total strength of selection' (Alberti et al., 2017).

Cities are increasingly recognized as agents of evolutionary change that can provide unique insight on patterns of evolution, specifically rapid adaptation (Donihue & Lambert, 2015; Johnson & Munshi-South, 2017; Lambert et al., 2021; Thompson et al., 2018). Cities occupy only 3% of Earth's landmass, while hosting more than half of the human population. The UN projects that cities will continue to grow, with 68% of the population living in cities by 2050 (United Nations, 2019). The rapid pace of urbanization creates many challenges for an ever-growing urban human population, as well as for preserving urban biodiversity. The nascent field of urban evolutionary biology studies adaptation in cities compared to less anthropogenic habitats, in order to predict how wildlife can cope with growing urbanization, and using cities as laboratories to explore eco-evolutionary processes involved in species rapid adaptation (Szulkin, Munshi-South, & Charmantier, 2020).

Theoretically, the many constraints associated with urban life, such as reduced access to high-quality food resources or shelter and strong disturbances by humans, cars and domestic pets, could shift the fitness landscape, decreasing mean absolute fitness, and increasing maladaptation and the opportunity for selection (fig. 1 in Fugere & Hendry, 2018). In contrast, urban conditions could also lead to relaxed selection. First, this can happen if human habitat alteration reduces the fitness advantage of a trait. For example, eutrophication and algae invasion in the Baltic Sea have rendered the male red nuptial coloration of three-spined sticklebacks (*Gasterosteus aculeatus*) ineffective in sexual courtship due to poor visibility, resulting in weaker natural selection (Candolin et al., 2007). Second, urban environments can be more homogeneous than natural habitats for some species, buffering organisms from environmental variation. For instance, the urban heat island (UHI) effect keeps cities warmer during extreme cold (Yang & Bou-Zeid, 2018). Such buffering could decrease among-individual variation in fitness and relax selection pressures (see e.g. Rodewald & Arcese, 2017). Note that a given city characteristic such as the UHI can have both positive and negative influences on fitness depending on the species or the season (see e.g. in humans, Macintyre et al., 2021).

Cronin et al. (2022) reviewed evidence for divergent sexual selection in urban habitats and drivers, such as pollution or resource availability, that shape selection pressures acting on sexual traits. They identified 104 studies published between 1980 and 2021, providing insight on urban influences on sexual signalling (tab. S1 in Cronin et al., 2022). For instance, trade-offs between signal transmission and attractiveness lead to altered male songs in urban

areas, with higher minimum frequencies for several bird species (Dowling et al., 2012; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006). Although interpreted in the light of new sexual selection pressures (e.g. selection for increased signal transmission in the above example of male bird song), the majority of these case studies provide no estimates of the strength of selection.

Natural selection can be defined in 'purely phenotypic terms' (Arnold & Wade, 1984) because it involves differences in fitness resulting from differences in phenotypic traits. As such, selection has been historically approached by estimating the covariance between a phenotype and relative fitness (Price, 1970). Another approach examining natural selection in urban habitats determines how genomes have been shaped by urban adaptation versus urban-specific demography, gene flow or drift (Johnson et al., 2018). While these attempts rarely produce robust conclusions on natural selection without associated fitness measures, studies providing genetic selection coefficients can compare the magnitude of natural selection acting on genetic variants in urban versus non-urban habitats. Thurman and Barrett (2016) gathered 3416 genetic selection coefficients published in 79 studies across habitat types, providing fascinating insight into how selection shapes genomes, for instance revealing stronger selection over shorter timescales. They highlighted the limited data available compared to the huge potential to estimate similar genetic selection coefficients across taxa and contexts. This study inspired us to perform a similar literature search, restricted to urban versus non-urban contexts, with the hope that Thurman and Barrett's call lead to numerous new estimates.

Recent reflections on the field of urban evolutionary biology underscore the low number of studies that have documented cases of biological adaptation to urban environments (Lambert et al., 2021) and the difficulty in reaching general conclusions on how urbanization affects natural selection (Verrelli et al., 2022). The answer to this latter question can depend on the target of selection, the spatial and temporal scales considered, the age and history of cities, and the numerous agents of selection in cities such as air, light and sound pollution (Verrelli et al., 2022; Winchell et al., 2022). The aim of our study is to focus on the fundamental process of natural selection which drives adaptation, and assess how urbanization alters selection, via (1) evaluating whether the strength of phenotypic selection is generally stronger or weaker in cities when compared to natural habitats and (2) measuring the force of urban-related selection on adaptive genomic variants. We reviewed the literature comparing coefficients of natural selection in urban and non-urban habitats using both phenotypic and genomic approaches with the initial aim of conducting meta-analyses to quantitatively assess trends for given traits or taxa. The scarcity of studies prevented such an analysis, and thus, we provide a qualitative assessment of how natural selection can differ in urban versus non-urban environments and outline a road-map for how future studies should provide standardized metrics to facilitate mega- or meta-analyses and explore generalized effects of urbanization on selection.

## 2 | URBAN NATURAL SELECTION ON WILD PHENOTYPES

Understanding how natural selection varies across wild populations, but also in time, is considered a central question in evolutionary ecology (Bell, 2010; Hoekstra et al., 2001; Morrissey & Hadfield, 2012; Siepielski et al., 2009). It has led to an abundant literature, in particular following the publication of Lande and Arnold's (1983) accessible introduction on how to measure linear and non-linear selection differentials/gradients using multivariate regression on individual phenotypic and fitness data (Svensson, 2023). A selection differential reflects the total selection acting on a single trait regardless of other potentially selected traits, while a selection gradient accounts for several traits being involved in the selection episode using a multivariate analysis (Mittell & Morrissey, 2024).

To determine whether urbanization affects the strength of selection, we first synthesized studies on phenotypic traits that (i) estimated selection coefficients i.e. selection differentials and gradients in urban and non-urban environments and (ii) provided compelling evidence for altered urban selection. Studies reviewed in Section 2.1. were found by searching Google Scholar for studies that cited Lande and Arnold (1983; following approach in Fugere & Hendry, 2018) and mentioned either urban\*, city\*, town\*, or metro\* (conducted 15 January 2024,  $n=6$  relevant studies out of 439 hits, see full list in Table S1). We also conducted a Web of Science Core collection search (CNRS institution access in Montpellier, France, on 15 January 2024, see Table S2 for full search terms) that included articles containing urban-related search terms (Topic = 'urban\* OR city\* or town\* OR metro\*') and either 'selection gradient\*' or 'selection differential\*' across all fields, which did not return any new article. We also included two other relevant studies that did not appear in either of these searches and were identified by reviewing the reference lists of relevant studies ( $n=2$ ; Badyaev et al., 2008; Branston et al., 2021). From the Google Scholar search, we identified eight studies that estimated coefficients of selection but did not provide a comparison to non-urban habitats (Gregoire et al., 2004; Houle et al., 2020; Lambrecht et al., 2016; Price et al., 2008; Ryder et al., 2012; Sol et al., 2003; Spear et al., 2023; Yeh & Price, 2004). For instance, larger size was under strong selection in holy hawksbeard (*Crepis sancta*) in urban environments (Lambrecht et al., 2016), but it is unknown whether selection for plant size is stronger or weaker for this species outside the urban setting. While these studies may be important for future meta-analyses, they are not discussed further in our comparative approach.

Overall, studies estimating wild selection coefficients were all conducted in avian or plant taxa ( $n=8$ , five studies on three avian species and three studies on three plant species; Figure 1; Table 1; Table S3), with a particular focus on morphological and phenological traits. The modest number of studies found highlights a crucial gap of knowledge on the magnitude of urban/non-urban differences in selection, as well as on the specific urban drivers that modify the strength of selection, which are often speculated upon but very rarely demonstrated.

## 2.1 | Phenotypic selection differentials and gradients

### 2.1.1 | Stronger urban natural selection

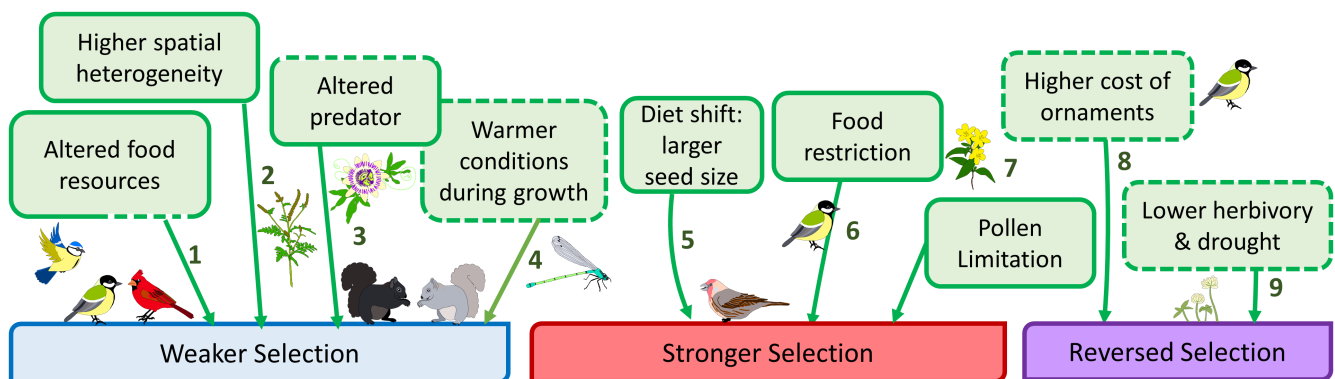
Stronger estimates of urban selection have so far been reported in bird and plant species (Table 1). The limited number of studies in Table 1 suggests that in birds, selection in urban habitats may more strongly act on morphological traits than behaviour or life-history traits, with the underlying drivers often linked to changes in urban diet. Urban bird feeding activities have shifted urban diets towards larger seed resources which has led to strong selection favouring longer bills in urban house finches (*Carpodacus mexicanus*) compared to desert finches (Badyaev et al., 2008). Another example from great tits (*Parus major*) along an urbanization gradient in Warsaw revealed stronger selection in more urbanized areas favouring higher body mass at hatching (Corsini et al., 2021), most likely related to the reduction in food resources (Seress et al., 2018).

As in birds, evidence for stronger urban selection in plants has been documented in morphology, related to increases in floral size. In the Yellow jessamine (*Gelsemium sempervirens*), selection for larger floral displays is significantly stronger in urban areas compared to non-urban areas, perhaps driven by reductions in urban pollinators (Irwin et al., 2018). Although the study supports stronger urban selection for floral display size, the authors highlight that they find only modest selection estimates for the other traits considered, suggesting that urbanization may not contribute to sweeping changes in phenotypic selection as commonly expected (Irwin et al., 2018).

### 2.1.2 | Weaker urban natural selection

Evidence in birds for weaker urban selection come from two tit species, but range across morphological, life-history, and behavioural traits. Urban great tits in the city of Montpellier tend to be smaller, faster explorers, more aggressive, and more stressed during handling, and tend to lay earlier and smaller clutches than tits living in a nearby forest habitat (Caizergues, Gregoire, et al., 2022; Charmantier et al., 2017). Selection gradients across these traits were overall weak in both habitats and, in some cases, patterns of selection were in the opposite direction to the documented phenotypic divergence (e.g. for breeding phenology, Caizergues et al., 2018). In higher latitude populations of blue tits around Glasgow, there is selection for earlier lay dates and larger clutches in both urban and forest habitats but, again, the strength of selection on these traits was significantly weaker in urban areas (Branston et al., 2021). The authors show that their urban study sites possess fewer caterpillars and hypothesise that weaker environmental cues in urban areas could contribute to relaxed urban selection on phenology (Branston et al., 2021).

We describe above that urban selection can be stronger on floral display size, but we find support for weaker urban selection on other plant morphological traits. Bird visitation was found to exert selection on fruit crop size across populations of the blue passionflower (*Passiflora caerulea*), but this selection was weaker in the urban and semi-urban populations, and strongest in the rural population (Palacio & Ordano, 2023). The authors suggest that this relaxed urban selection could be a result of either (i) urban populations being closer to the phenotypic optimum as they tended to have larger average fruit crop sizes or (ii) generalist bird species in urban areas being less selective of which fruits (and associated traits) they forage. This calls for an integration of



**FIGURE 1** Illustrating some studies that have demonstrated divergent natural selection in urban habitats, with potential explanations regarding the agents that can lead to weaker, stronger, or reversed natural selection in cities. Studies either compared selection differentials/gradients between urban and non-urban habitats (solid lines, discussed in Section 2.1), or used other approaches (dotted lines, Section 2.2). List of species and references: 1: Great tit *Parus major* in Caizergues et al. (2018); Blue tit *Cyanistes caeruleus* in Branston et al. (2021); Northern Cardinal *Cardinalis cardinalis* in Rodewald et al. (2011); 2: Common ragweed *Ambrosia artemisiifolia* in Gorton et al. (2018); 3: Blue passionflower *Passiflora caerulea* in Palacio and Ordano (2023); Eastern gray squirrel *Sciurus carolinensis* in Cosentino et al. (2023); 4: Damsselfly *Coenagrion puella* in Tüzün et al. (2017); 5: House finches *Carpodacus mexicanus* in Badyaev et al. (2008); 6: Great tit in Corsini et al. (2021); 7: Yellow jessamine *Gelsemium sempervirens* in Irwin et al. (2018); 8: Great tit in Senar et al. (2014); 9: White clover *Trifolium repens* in Santangelo et al. (2022). All drawings from MJT.

TABLE 1 Studies estimating selection differentials or gradients in urban and non-urban environments.

Taxa	Species	Phenotypes	Fitness proxy	Results	Reference
Birds	House finch ( <i>Carpodacus mexicanus</i> )	Morphology: Bill length, width, depth	Survival: Survival to following year	Stronger urban directional selection	Badyaev et al. (2008)
	Great tit ( <i>Parus major</i> )	Morphology: Body mass	Survival: Survival to fledging	Stronger urban selection in both species, but urban selection significantly higher only in great tits	Corsini et al. (2021)
	Blue tit ( <i>Cyanistes caeruleus</i> )				
	Great tit ( <i>Parus major</i> )	Morphology: Body mass, wing length, tail length Life history: Lay date, clutch size	Reproduction: Number of fledglings	Selection on traits overall weak in both habitats, but significantly weaker urban selection for lay date and body mass (males)	Caizergues et al. (2018)
	Great tit ( <i>Parus major</i> )	Behaviour: Exploration, aggression, stress response	Reproduction: Number of fledglings	Selection on traits overall weak in both habitats, but significantly weaker urban selection for exploration (males)	Caizergues, Gregoire, et al. (2022)
	Great tit ( <i>Parus major</i> ) Blue tit ( <i>Cyanistes caeruleus</i> )	Life history: Lay date, clutch size	Reproduction: Number of fledglings	Selection was significantly stronger in the forest for both traits only in blue tits, no significant difference in great tits.	Branston et al. (2021)
Plants	Yellow jessamine ( <i>Gelsemium sempervirens</i> )	Morphology: Floral size, display size & shape Physiology: Chemical defence	Reproduction: Seeds per plant	Significantly stronger urban selection for larger floral display size	Irwin et al. (2018)
	Blue passionflower ( <i>Passiflora caerulea</i> )	Morphology: Fruit diameter, mean seed number, crop size, peel carbohydrate content	Reproduction: Fruit removal	Weaker urban and semiurban selection for fruit crop size, but not statistically compared	Palacio and Ordano (2023)
	Common ragweed ( <i>Ambrosia artemisiifolia</i> )	Morphology: Plant height Phenology: Transition to reproduction, first open male flower, male to female flower	Reproduction: Number of flowers & fruits	Net selection favoured larger plants and earlier phenology overall, but stronger selection on foreign genotypes	Gorton et al. (2018)

Note: Order follows discussion in the main text.

Abbreviations: CMR, capture-mark-recapture; ISA, Impervious surface area.

species interactions to unravel the agents driving novel selection pressures in cities. In another example, selection favoured taller height and earlier phenology across common ragweeds (*Ambrosia artemisiifolia*) of urban and rural origins planted in both urban and rural study sites (Gorton et al., 2018). Genetic differentiation and stronger selection on foreign genotypes provide consistent support for local adaptation in ragweed, although plants from rural origins tended to have higher overall lifetime fitness when reared in both urban and rural study sites providing conflicting support (Gorton et al., 2018). The authors suggest this latter finding could result from weaker selection in the urban environment, potentially because urban habitats are more spatially heterogeneous (Gorton et al., 2018).

### 2.1.3 | Insight from urban phenotypic selection gradients

Across the studies in Table 1, no obvious generalizations have emerged that enable directional predictions on how urbanization impacts

selection across different traits and species. Our goal to conduct a formal quantitative analysis is not achievable given the few studies that have quantified selection coefficients ( $n=8$ ). We list in the Supporting Information (Table S3) 200 effect sizes ( $n=101$  urban and 99 non-urban) of linear selection gradients and differentials reported in these studies. We consider this a first step to inspire research interest in reporting these selection coefficients and their associated uncertainty, so that meta-analyses can be conducted in the future. Descriptively, the median (absolute) urban and non-urban selection gradients are similar ( $n$  urban=70 with median: 0.091, range: 0.0001–1.06;  $n$  non-urban=68 with median: 0.10, range: 0.004–1.37), and within the range of previously reported summaries of selection in natural populations (see e.g. Kingsolver et al., 2012; Morrissey & Hadfield, 2012). Similar median strength of selection between urban and non-urban habitats is somewhat unsurprising given there is evidence of both stronger and weaker urban phenotypic selection (as summarized above) and selection estimation is classically associated with large measurement error (e.g. Dingemanse et al., 2021). Overall, our summary on phenotypic coefficients of selection implies that we so far are unable to generalize on

how urbanization impacts the strength of selection. Further comparative research of selection in and outside cities across diverse systems is needed before this conclusion can be re-addressed and any generalities can emerge.

## 2.2 | Compelling evidence of modified selection

Since the literature search conducted above was not conclusive regarding differences in selection differentials or gradients between non-urban and urban areas, we further discuss studies that offer complementary insights on this topic. While these studies do not allow a quantitative comparison across species and contexts, they do provide unique insight into the mechanisms that may drive novel, stronger or weaker selection in cities. Demonstrating the causal agents of selection has always been a great challenge in evolutionary ecology, and it is usually not possible to firmly identify the drivers via a correlational approach (Mitchell-Olds & Shaw, 1987; Svensson, 2023). Cities are characterized by multifarious urban stressors such as multiple forms of pollution, heat, and altered and fragmented habitats (Diamond & Martin, 2021). Only experimental manipulations such as alteration of the biotic (e.g. predation pressure) or abiotic (e.g. temperature) variables can clearly identify agents driving differences in selection in urban environments (MacColl, 2011; Wade & Kalisz, 1990).

### 2.2.1 | Relaxed selection under altered resource and predator regimes

In their extensive review on the effects of urbanization on sexual selection, Cronin et al. (Cronin et al., 2022) cited resource availability as one of the main biotic drivers influencing the strength and form of sexual selection in an urban context. While food is necessary for somatic growth and maintenance, it is also a key determinant of colourful ornaments. In the Northern Cardinal *Cardinalis cardinalis*, the red plumage of males is produced from carotenoid pigments that are found in their diet. A study of northern cardinals by Rodewald et al. (2011) across a rural-urban gradient in Ohio, USA, revealed that in more urban landscapes, brightness of male plumage no longer correlated with breeding phenology or reproductive success. The authors suggest that this relaxed selection for colour arises because of the over-abundance of carotenoid-rich exotic fruits in cities, such as honeysuckles. We find this example particularly striking because in other bird species with carotenoid-related colours, urban birds are generally paler (Janas et al., 2024), although with strong variation across cities, and no insight yet on the force of natural or sexual selection on these colours (Salmón et al., 2023).

One of our favourite demonstrations of relaxed selection in cities was recently published and echoes the iconic study of industrial melanism in the peppered moth *Biston betularia* in industrial England (see e.g. Cook & Saccheri, 2013). Following observations of parallel high prevalence of melanic eastern gray

squirrels (*Sciurus carolinensis*) across 43 cities in North America, Cosentino et al. (2023) translocated 76 gray squirrels from urban areas in Syracuse to both urban and rural novel areas. The subsequent monitoring revealed that while gray squirrels had much higher survival than melanic squirrels in rural habitats, there was no such evidence for survival selection in the city. The authors favour the hypothesis that weaker selection against the conspicuous melanic morph in the city results from lower predation and human hunting pressure.

Finally, the role of altered predator communities is also cited as a possible agent of relaxed selection for fast growth rates in urban damselflies *Coenagrion puella* (Tüzün et al., 2017). Note that while experimental approaches such as this common garden on damselflies are very powerful to test for urban local adaptation (Lambert et al., 2021), they do not provide adequate quantitative measures of natural selection.

### 2.2.2 | Reversed selection and identifying multiple agents of selection

Evidence for reversed selection in urban habitats is very scarce but it was shown in a common urban-dweller, the great tit. Using 17 years of capture-mark-recapture data and measures of the size of the black breast stripe of male great tits in and around Barcelona, Senar et al. (2014) found that forest males with larger stripes had higher survival while the reverse was true in urban males. While the size of male black ties has been positively associated with dominance status (e.g. Jarvi & Bakken, 1984), tie size is also negatively correlated with exploration speed (Nicolaus et al., 2016). Senar thus hypothesizes that smaller ties in city birds is likely a by-product of selection on personality (J. C. Senar, pers. com.), which aligns with findings that urban great tits are bolder and faster explorers (e.g. Riyahi et al., 2017).

A global study of the white clover (*Trifolium repens*) illustrates the difficult task of identifying agents of selection in a complex urban system. A large-scale study of 20 Canadian cities revealed parallel clines with decreased plant production of hydrogen cyanide (HCN) in response to urbanization, indicating parallel evolution resulting from parallel selection favouring lower chemical defence in cities (Johnson et al., 2018). Despite the large number of cities in this study, agents of selection causing these evolved differences remained unclear. In an even larger scale study across a monumental 160 cities, Santangelo and colleagues analysed environmental predictors of HCN clines, concluding that herbivory selected for higher HCN in rural areas while lower drought selected for lower HCN in urban areas (Santangelo et al., 2022).

It is sobering to note that for most studies discussed in this section, even with extensive efforts across decades, agents of selection inducing new selective forces in urban environments remain hypothetical interpretations from field experts. We also note that, and again despite tremendous effort, most of these studies do not measure individual fitness and hence could not be included in a

quantitative meta-analysis of standardized selection estimates. In comparison to the demanding challenge of collecting data that allow estimating phenotypic selection coefficients, selection coefficients from genomic data may be more tractable for many taxa.

### 3 | GENOMIC INSIGHT ON MEASURING URBAN SELECTION COEFFICIENTS

Estimates of genetic selection coefficients can provide important knowledge on the nature of selection acting on adaptive traits and their underlying genetic architecture. These estimates can be complementary to selection coefficient estimates based on phenotypic and fitness data, depending on whether such phenotypic-based approaches have already been performed or are even possible. While linking phenotypes and fitness measured in the wild can provide insights into the functional significance of specific traits in a given environment, genomic selection coefficients quantify the overall past strength of natural selection on specific genetic variants, based on genomic data only. While genetic selection coefficients are often seen as analogous to phenotypic selection differentials, comparing discrepancies between them can inform on pleiotropic, epistatic, or linkage disequilibrium effects (Thurman & Barrett, 2016). In addition, detecting stabilizing selection is a very challenging task when using genetic data because allele frequencies remain the same under such selection regimes.

Genetic selection coefficients for mono- or oligo-genic traits can be measured by genotyping one of a few candidate loci previously identified as being under selection and/or associated with phenotypic variation. Advances in genotyping methods, principally through democratization of high-throughput sequencing, present new opportunities to scan genomes, detect loci under selection and/or associated with phenotypic variation, and estimate genetic selection coefficients on polygenic traits for natural populations of non-model species (Bank et al., 2014; Barrett & Hoekstra, 2011; Manel et al., 2016; Matz, 2018; Nielsen, 2005). Note that even with novel polygenic approaches, the genetic variation uncovered often explain only a small percentage of phenotypic variance. In the next section, we describe general methods for calculating genetic selection coefficients, then review their application in an urban context. Finally, we highlight important gaps in the current literature and we propose in the next section future steps that can be taken to help advance our knowledge of selection in urban environments.

#### 3.1 | Overview of genetic approaches to measure selection coefficients

As the scope of our article is to review the state of the literature and not to describe in detail the methodology for calculating selection coefficients, we refer interested readers to comprehensive reviews of popular and useful methods for calculating genetic selection coefficients by Linnen and Hoekstra (2009) and Bank et al. (2014).

In brief, the most straightforward strategies for measuring selection based on genomic data depend on the availability of measures of individual fitness (or fitness-related traits) and individual genotypes for causal loci or genome-wide variants (e.g. SNPs). In the simplest cases, such as at a single Mendelian locus causing discrete polymorphic phenotypes, selection coefficients can be calculated from estimates of the relative fitness ( $w$ ) for a given genotype (Eanes, 1999). Advances in genomic techniques now allow such estimates for quantitative trait loci and further, can aid in discovery of candidate loci, circumventing the need for prior knowledge of causal loci. One popular contemporary strategy is to use genome scans or Genome-Wide Association Study (GWAS) to identify loci underlying variation in fitness or fitness-related traits, and then measure selection at these candidate loci by associating allelic variation and individual fitness. For example, Bérénos et al. (2015) combined genomic SNP data with fitness and phenotypic measures to investigate the genetic architecture of body size traits. The authors used a GWAS to identify SNPs associated with body size (i.e. hind length), tested the association between fitness and genotypes for outlier SNPs, then estimated selection coefficients at these SNPs. Their study illustrates how contemporary population genomics techniques paired with traditional phenotypic and fitness measures can both facilitate the discovery of candidate loci underlying quantitative traits and improve our understanding of how selection affects these loci in natural populations.

Many studies may lack fitness and phenotypic data. In these cases, selection coefficients can be calculated from changes in allelic frequencies over time (i.e. multiple generations) or over geographic space (i.e. clines). If the candidate gene is unknown, it can be analysed by applying first genome scans (methods reviewed in Hohenlohe et al., 2010) and then by estimating selection coefficient on identified outlier loci. Otherwise the selection coefficient for known candidate genes can be directly estimated. Selection coefficients are estimated by computing the probability of the underlying changes in allele frequencies over multiple generations or geographic locations, often using a likelihood-based approach (e.g. software package SelEstim; Vitalis et al., 2014) or approximate Bayesian computation (ABC) approaches (e.g. Bank et al., 2014; Stern et al., 2019). Importantly, these methods are in general very sensitive to sample size (Pinsky et al., 2021) as well as the spatial and/or temporal distribution of sampling. As an example of this strategy relying on genomic data only, Walden et al. (2020) estimated selection coefficients at genes implicated in evolutionary response to spatially heterogeneous climatic conditions in *Arabidopsis lyrata*, first using GWAS and Environmental Association Analysis (EAA) to identify outlier SNPs and genes associated with local climatic variation, then estimating mean genomic selection coefficients for these loci using SelEstim (Vitalis et al., 2014). Their results revealed increased selection coefficients for environment-associated genes compared to coefficients for genes that were not associated with environment, suggesting that these genes have importance in climate adaptation. These

methods could be easily extended to urban contexts, where temperatures persistently rise, and our comprehension of the selection pressures induced by these escalating temperatures remains constrained. Consequently, in the absence of accessible phenotype and fitness measures, this approach affords the potential to discern genes intricately linked to climate adaptation and facilitates the estimation and comparison of selection intensities between urban and natural environments.

### 3.2 | A review of genomic selection coefficients in the wild urban context

While genomic selection coefficients can provide valuable insight to understanding basic questions in evolutionary biology, there remains limited knowledge about the distribution of selection coefficients ( $s$ ) in natural populations. A meta-analysis by Thurman and Barrett (2016) aimed to quantify natural selection at the genetic level, reviewing over 2000 papers and ultimately extracting ~3000 estimates from 79 studies. While their analysis provided valuable insight into the magnitude and tempo of selection in natural environments, for example, suggesting that selection is stronger over shorter time-scales, their study also underscored that a critical lack of published selection coefficients constrained their ability to conclusively address these topics. We anticipated that in the years since Thurman and Barrett's review, an increased number of studies would report genomic selection coefficients, including studies set in an urban context. Thus, our objective was to replicate their meta-analysis and literature search to retrieve and analyse estimates of selection, with a focus on estimates of selection coefficients in urban contexts.

#### 3.2.1 | Systematic review and data extraction

We identified relevant papers with literature searches using the Web of Science Core Collection (conducted 8 November 2023, see Table S2 for full search terms), filtering results to include only primary articles in evolutionary biology containing urban-related search terms (Document Types: Article; Research Areas: Evolutionary Biology; Topic = 'urban\* OR city\* or town\* OR metro\*'). We conducted three independent searches using different sets of search terms. In Search 1, we specified key terms used by Thurman and Barrett (2016) to find published estimates of natural selection acting at the genetic level: Topic = ('selection coefficient\* OR genotyp\* selection OR adapt\* gene'). In Search 2, we broadened our criteria to include selection gradients: Topic = ('selection coefficient OR selection gradient'). In Search 3, we targeted potentially relevant papers by specifying popular approaches for quantifying the strength of selection from genomic data, as identified from Linnen and Hoekstra's (2009) review: Topic = ('MK test OR McDonald Kreitman test OR McDonald-Kreitman test OR dn/ds test OR nonsynonymous substitutions synonymous substitutions OR allele frequenc\*

ecotone OR allele frequenc\* cline width OR CLR test OR composite-likelihood-ratio test'). These searches returned CLR 264, 15, and 133 articles respectively, for a total of 412 papers.

De-duplication resulted in 383 articles that we screened for inclusion (see Table S4). Our initial criteria for inclusion in our review were that each study: (1) provided a selection coefficient or selection gradient for a genetic unit (allele, SNP, QTL, chromosome, etc); (2) provided the selection statistic for both an urban and a non-urban population; and (3) focused on natural populations (e.g. not laboratory or domesticated plants and animals). No paper met all criteria, however, so we relaxed our criteria to encompass studies that (1) provided genomic evidence for selection or selection coefficients/gradients estimated from genomic data; (2) provided this genomic evidence for at least one urban population; and (3) focused on natural populations.

#### 3.2.2 | Insights from the literature review and discussion

Of the 383 articles that we reviewed, no paper met all initial criteria for inclusion, and only 34 (9.6%) met our relaxed criteria for inclusion. Many of the remaining 321 articles were irrelevant to our focus despite our specified criteria (e.g. they concerned agricultural populations, lacked urban context, or did not report genetic data). Our difficulty in identifying relevant studies mirrors challenges reported by Thurman & Barrett in their meta-analysis (Thurman & Barrett, 2016): of the 2200 studies reviewed for inclusion, they were able to accept only 79 (3.5%). Anticipating this challenge, we sought to improve the relevancy of our results and the efficacy of our search by complementing Thurman & Barrett's key terms (Search 1) with independent searches for more broad key terms (Search 2) and for key terms explicitly targeting well known and long-used methods for calculating genetic selection coefficients (Search 3). Still, we retrieved few relevant papers. In fact, Search 2 and Search 3 combined were less successful than Search 1: while Search 1 returned 29 relevant papers out of 264 total papers (11.0%), Search 2 returned only 1 relevant paper out of 15 total papers (6.7%) while Search 3 returned only 2 relevant papers out of 133 total studies (1.5%). Together, however, these three searches incorporated a range of both broad and targeted keywords. We therefore suggest that our detection of few relevant papers reflects an apparent lack of genetic selection coefficients reported in the urban eco-evolutionary literature.

The 34 papers we retained for our study (Table S5) included urban-associated genomic 'signatures of selection', e.g. using genomic scans to identify candidate SNPs for divergent selection between urban and non-urban environments (Hohenlohe et al., 2010; Nielsen, 2005). Six papers of these 34 papers presented genomic data that could be used to estimate the strength of selection. Of these, five studies reported urban/non-urban genetic clines; however, none of these papers used the documented genetic clines to



calculate selection coefficients (Linnen & Hoekstra, 2009). Only 1 study of the 34 reported selection coefficients; however, this was for a single urban population without a non-urban statistical complement (see Box 1).

## 4 | ROADMAP FOR FUTURE PHENOTYPIC AND GENOMIC STUDIES

This review has revealed how difficult it is to presently conduct a quantitative comparative analysis of studies exploring urban versus non-urban natural selection, both at the phenotypic and the genomic levels, using a systematic literature review and meta-analytical approach. What would it take for future studies to allow such a quantitative approach and derive more general interpretations on which traits in which taxa can be expected to be under stronger, weaker or reversed selection in the urban context?

### 4.1 | Facing the challenge of standardized estimations of natural selection

For meta-analysts to combine summary statistics on urban and non-urban natural selection, the primary studies estimating selection should ideally integrate all insight from the vast literature that delivers guidance for adequate statistical approaches and provide coefficients with their error estimation informing on accuracy. Our objective here is not to provide an exhaustive insight on how to measure natural selection in the wild as others have covered this extensively (Brodie et al., 1995; Linnen & Hoekstra, 2009; Stinchcombe et al., 2017). Table 2 provides a synthesized list of questions and challenges that must be addressed when estimating natural selection based on wild phenotypic and fitness data. These challenges are split into three categories: (1) Questions that need addressing at the start of any project measuring coefficients of natural selection, (2) Outstanding biological questions regarding what aspect of the trait-fitness relationship we want to measure, with specific questionings in the urban context, (3) Statistical challenges that make biological questions more difficult to answer. Note that there is subjectivity in whether a challenge is placed in the second or third category as many challenges in the third section can be considered outstanding questions of focal interest (e.g. spatio-temporal patterns of selection).

*In fine*, is it possible to gather comparable estimates of natural selection in the urban context despite 'the tremendous quantitative and statistical sophistication that is being brought to measuring selection on phenotypes and genomes' (Stinchcombe et al., 2017)? The long list and associated (non-exhaustive) references in Table 2 are sobering and many of the issues raised here could be broken down into a number of sub-considerations. Since long-term monitorings of urban populations are often much shorter than comparable datasets in natural settings, power issues will likely be one of the top challenges to face.

### BOX 1 A single study to date reporting urban genomic selection coefficient

Baltzegar et al. (2021) studied the evolution of a knock-down resistance (*kdr* haplotype) in the mosquito *Aedes aegypti* in response to insecticide use in the city of Iquitos (Peru). The frequency of resistant alleles was expected to increase over time, with positive selection coefficients induced by insecticide exposure. The authors genotyped the *kdr* mutations associated with pyrethroid resistance, in 9882 mosquitoes sampled in several locations in Iquitos City before/during/after the use of insecticides. They then estimated selection coefficients of the resistance alleles at each locus using the Wright-Fisher approximate Bayesian computation method for temporally sampled data (Foll et al., 2015). The frequency of *kdr* resistance mutations increased rapidly after insecticides exposure, with very large selection coefficients of 0.313 (95% CI: 0.007, 0.821) and 0.485 (95% CI: 0.145, 0.969) for the two resistance mutations. The authors discuss that these selection coefficients may be underestimated because of several violations of the model's assumptions, including non-independence of the mutations and spatio-temporal heterogeneity of the selection pressure. The authors also note that, although frequencies of resistant alleles shifted quickly during the study period, genetic heterogeneity existed not only at the citywide scale but also on a very fine scale within the city. In the scope of our review, we note that this example does not address the question of whether urbanization leads to stronger, weaker or reversed selection but that a comparison with similar estimates outside the urban context would allow conclusions on urban-specific selection.

### 4.2 | Towards more selection coefficient estimations in genomic studies of urban adaptation

Many challenges outlined in Table 2 are related to measuring and analysing fitness data, and hence will not apply when adopting a genomic perspective on selection. While population genomic studies performed in urban contexts did not report selection coefficients at loci underlying fitness variation, many studies did identify putative genomic footprints of selection. These studies mostly followed a similar strategy, comparing populations in urban versus non-urban environments to (1) identify candidate SNPs under divergent selection through multiple approaches, and (2) identify biological pathways and functions involved in adaptation to urban environments (Caizergues, Le Luyer, et al., 2022; Harris & Munshi-South, 2017; Theodorou et al., 2018). To provide more selection coefficients, a simple first step will be to extend studies that have already identified potential genomic footprints of selection and/

**TABLE 2** The challenges of estimating natural selection in wild urban and non-urban populations and associated literature.

The challenge	References addressing it
<b>1. Initial fundamental considerations:</b>	
How to estimate total selection over a life cycle?	Arnold and Wade (1984), Charlesworth (1993), Lande (1982) and Shaw and Geyer (2010)
What is the best estimate of fitness?	Arnold (1983) and Franklin and Morrissey (2017)
Do we have sufficient power to detect selection?	Hersch and Phillips (2004) and Mitchell-Olds and Shaw (1987)
Which statistical methodology to implement depending on the trait-fitness relationship we aim to measure?	Janzen and Stern (1998), Morrissey (2014a), Morrissey and Goudie (2022) and Morrissey and Sakrejda (2013)
How to standardize fitness and traits?	Hereford et al. (2004) and Lande and Arnold (1983)
<b>2. How to best estimate:</b>	
Direct and indirect selection, and causal pathways e.g. <i>What is the shape and force of natural selection acting on a focal trait in cities versus non-urban habitats?</i>	Arnold and Wade (1984), Henshaw et al. (2020), Lande and Arnold (1983), Morrissey (2014b) and Scheiner et al. (2000)
Linear and non-linear selection e.g. <i>Is there an optimum phenotype in the urban environment?</i>	Henshaw and Zemel (2017), Lande and Arnold (1983) and Stinchcombe et al. (2008)
Environmental sensitivity of selection e.g. <i>What causes novel selection in the city?</i>	Chevin et al. (2015), MacColl (2011) and Wade and Kalisz (1990)
<b>3. How to best account for:</b>	
Multicollinearity	Chong et al. (2018), Lande and Arnold (1983), Mitchell-Olds and Shaw (1987), Morrissey (2014a) and Morrissey and Ruxton (2018)
Non-Gaussian trait distributions	Bonamour et al. (2017), de Villemereuil (2018), de Villemereuil et al. (2016) and Pick et al. (2022)
Non-Gaussian fitness distribution	Shaw and Geyer (2010)
Uncertainty and sampling error (in particular for meta-analyses)	Morrissey (2016), Morrissey and Hadfield (2012) and Stinchcombe et al. (2014)
The problem of environmental covariance between trait and fitness	Kruuk et al. (2003), Morrissey et al. (2010), Morrissey and Henshaw (2022) and Rausher (1992)
Individual interactions	Hadfield and Thomson (2017)
Spatial autocorrelation in fitness	Marrot et al. (2015)
Temporal autocorrelation and fluctuating selection	Chevin et al. (2015) and de Villemereuil et al. (2020)
The missing traits and the invisible fraction	Grafen (1988), Hadfield (2008) and Mittell and Morrissey (2024)
Trait variation across lifetime (i.e. labile traits)	Araya-Ajoy et al. (2023) and Dingemanse et al. (2021)

or loci associated to phenotypic variations to include estimates of selection coefficients, for example, using the SelEstim software (Vitalis et al., 2014) and other aforementioned methods (Section 3.1). Second, the statistical methods for calculating selection coefficients usually require large sample sizes, hence more comprehensive sampling—of large populations, multiple spatial

and/or temporal points, and ideally, with phenotypic and fitness measures—would allow more precise estimates of genetic selection coefficients.

While genomic studies usually lack fitness estimation, thus limiting the scope for adaptive interpretations of signatures of selection, they have the great advantage of providing insight on historical

patterns of selection that have shaped current phenotypic divergence and clines across urban gradients. In contrast, phenotypic approaches reviewed in section II provide insight on current patterns of natural selection with often strong variation across years and study areas for a given trait and taxa. Phenotypic and genomic approaches should therefore be used as complementary approaches to study urban-related natural selection at micro and macro-temporal scales.

### 4.3 | Final considerations: Fitness landscapes, opportunity for selection and mega-analyses

As a final look towards the future, we outline three different approaches that provide a different perspective on natural selection in urban areas.

First, rather than aiming to model a fitness-trait relationship using constraining parametric approaches, a more flexible approach could be to model the urban and non-urban fitness landscapes using nonparametric approaches such as cubic splines (Morrissey & Sakrejda, 2013; Schluter, 1988). Alternatively, one can use parametric approaches that relate more explicitly to theoretical predictions than do classic selection gradients from Lande and Arnold (1983). In particular, models of moving optimum are popular in theory on adaptation to changing environments (e.g. Kopp & Matuszewski, 2014) and can be inferred empirically (Chevin et al., 2015). Using such models, one could compare the location, width and height of the fitness peak between urban and non-urban populations in a comparable way to studies that have used this approach to investigate temporal fluctuations of selection (Chevin et al., 2015; de Villemereuil et al., 2020). Note that this fitness landscape approach also bears methodological limitations, e.g. it requires strong assumptions but also large sample sizes, to test how both the height and width of the fitness optimum may change, and as such it may not facilitate a quantitative comparison across urbanization gradients. It could however provide a powerful tool to partition selection episodes and to identify environmental drivers of urban-specific selection (Gamelon et al., 2018), and relate to the abundant literature on local adaptation involving quantitative traits (e.g. Kawecki & Ebert, 2004; Yeaman, 2015, 2022). Understanding how natural selection on a given character changes across different episodes of selection (e.g. viability selection and fertility selection; Walsh & Lynch, 2018) and different landscapes will provide crucial insight to understand how the trait may evolve in our ever changing city landscapes.

Second, while this review has covered studies that compare the relative strength of selection for a particular trait between urban and non-urban areas, we can also compare overall selection intensity between habitats. A comparison of overall selection between the two habitats could be better obtained using measures of the opportunity for selection  $I$ , or the variance in relative fitness (Arnold & Wade, 1984; Crow, 1958). Note that while  $I$  reflects the upper limit of the intensity of natural selection, recent findings show that it can be highly influenced by demographic stochasticity (Reed

et al., 2023), and it is likely that the continuously changing urban landscape where temporary construction sites are numerous, entails higher demographic stochasticity. Ultimately, we should be able to link  $I$  with population demography, and determine the overall link with selection as we classically measure it (i.e. on specific traits and at specific times in the life cycle), and total fitness. This is already an achievable goal in all studies that include fitness measures such as survival and/or reproductive success (e.g. number of flowers, fruits and seeds produced per plants in Irwin et al., 2018).

Third and finally, a promising solution for future quantitative approaches aiming at comparing urban and non-urban natural selection is to conduct mega-analyses on individual-based data for phenotypes, genomic data and fitness measures (Eisenhauer, 2021) rather than meta-analyses on heterogeneous non-comparable estimations. Mega-analyses pool raw data from multiple populations in order to use the same statistical treatment rather than gather estimates from different studies in meta-analyses. The success of such mega-analytical approaches rely heavily on data platforms and repositories that allow large-scale sharing of standardized data (such as SPI-birds, see Culina et al., 2021) following FAIR principles (aka Findability, Accessibility, Interoperability and Reusability, Wilkinson et al., 2016), while also promoting interactions and collaborations between data holders. A mega-analytic approach will not only address the challenges of estimating natural selection (Table 2) in a standardized way across all data, but will also allow the measurement of urban gradients in a homogeneous way rather than rely on heterogeneous measures of urbanization gathered from studies combined in a meta-analysis approach (Szulkin, Garroway, et al., 2020). We call here for use of mega-analyses in the near future as we envisage it will be a powerful way to assess how different natural selection can be in cities in a wide array of taxa and traits.

### AUTHOR CONTRIBUTIONS

From an original idea conceived by Anne Charmantier, all authors designed the research in a teamwork coordinated by Anne Charmantier; Megan J. Thompson performed the phenotypic reference search; Tracy Burkhard & Laura Gervais performed the genomic reference search; Sections 1 and 4 were written by Anne Charmantier, Section 2 by Megan J. Thompson & Anne Charmantier, Section 3 by Laura Gervais, Tracy Burkhard & Charles Perrier, and all authors contributed to editing the paper and revising it.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

This manuscript does not use any empirical data other than the literature searches that are all provided as supplementary tables.

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## REFERENCES

- Alberti, M., Marzluff, J., & Hunt, V. M. (2017). Urban driven phenotypic changes: Empirical observations and theoretical implications for eco-evolutionary feedback. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 372, 9.
- Araya-Ajoy, Y. G., Dingemans, N. J., Westneat, D. F., & Wright, J. (2023). The evolutionary ecology of variation in labile traits: Selection on its among- and within-individual components. *Evolution*, 77, 2246–2256.
- Arnold, S. J. (1983). Morphology, performance and fitness. *American Zoologist*, 23, 347–361.
- Arnold, S. J., & Wade, M. J. (1984). On the measurement of natural and sexual selection: Theory. *Evolution*, 38, 709–719.
- Badyaev, A. V., Young, R. L., Oh, K. P., & Addison, C. (2008). Evolution on a local scale: Developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution*, 62, 1951–1964.
- Baltzgar, J., Vella, M., Gunning, C., Vasquez, G., Astete, H., Stell, F., Fisher, M., Scott, T. W., Lenhart, A., Lloyd, A. L., Morrison, A., & Gould, F. (2021). Rapid evolution of knockdown resistance haplotypes in response to pyrethroid selection in *Aedes aegypti*. *Evolutionary Applications*, 14, 2098–2113.
- Bank, C., Ewing, G. B., Ferrer-Admetlla, A., Foll, M., & Jensen, J. D. (2014). Thinking too positive? Revisiting current methods of population genetic selection inference. *Trends in Genetics*, 30, 540–546.
- Barrett, R. D. H., & Hoekstra, H. E. (2011). Molecular spandrels: Tests of adaptation at the genetic level. *Nature Reviews Genetics*, 12, 767–780.
- Bell, G. (2010). Fluctuating selection: The perpetual renewal of adaptation in variable environments. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 365, 87–97.
- Berenos, C., Ellis, P. A., Pilkington, J. G., Lee, S. H., Gratten, J., & Pemberton, J. M. (2015). Heterogeneity of genetic architecture of body size traits in a free-living population. *Molecular Ecology*, 24, 1810–1830.
- Bonamour, S., Teplitsky, C., Charmantier, A., Crochet, P.-A., & Chevin, L.-M. (2017). Selection on skewed characters and the paradox of stasis. *Evolution*, 71, 2703–2713.
- Branston, C. J., Capilla-Lasheras, P., Pollock, C. J., Griffiths, K., White, S., & Dominoni, D. M. (2021). Urbanisation weakens selection on the timing of breeding and clutch size in blue tits but not in great tits. *Behavioral Ecology and Sociobiology*, 75, 12.
- Brodie, E. D., Moore, A. J., & Janzen, F. J. (1995). Visualizing and quantifying natural-selection. *Trends in Ecology & Evolution*, 10, 313–318.
- Caizergues, A. E., Gregoire, A., & Charmantier, A. (2018). Urban versus forest ecotypes are not explained by divergent reproductive selection. *Proceedings of the Royal Society B: Biological Sciences*, 285, 9.
- Caizergues, A. E., Gregoire, A., Choquet, R., Perret, S., & Charmantier, A. (2022). Are behaviour and stress-related phenotypes in urban birds adaptive? *Journal of Animal Ecology*, 91, 1627–1641.
- Caizergues, A. E., Le Luyer, J., Gregoire, A., Szulkin, M., Senar, J.-C., Charmantier, A., & Perrier, C. (2022). Epigenetics and the city: Non-parallel DNA methylation modifications across pairs of urban-forest great tit populations. *Evolutionary Applications*, 15, 149–165.
- Candolin, U., Salesto, T., & Evers, M. (2007). Changed environmental conditions weaken sexual selection in sticklebacks. *Journal of Evolutionary Biology*, 20, 233–239.
- Charlesworth, B. (1993). Natural selection on multivariate traits in age-structured populations. *Proceedings of the Royal Society B: Biological Sciences*, 251, 47–52.
- Charmantier, A., Demeyrier, V., Lambrechts, M., Perret, S., & Grégoire, A. (2017). Urbanization is associated with divergence in pace-of-life in great tits. *Frontiers in Ecology and Evolution*, 5, 53.
- Chevin, L. M., Visser, M. E., & Tufto, J. (2015). Estimating the variation, autocorrelation, and environmental sensitivity of phenotypic selection. *Evolution*, 69, 2319–2332.
- Chong, V. K., Fung, H. F., & Stinchcombe, J. R. (2018). A note on measuring natural selection on principal component scores. *Evolution Letters*, 2, 272–280.
- Cook, L. M., & Saccheri, I. J. (2013). The peppered moth and industrial melanism: Evolution of a natural selection case study. *Heredity*, 110, 207–212.
- Corsini, M., Schöll, E. M., Di Lecce, I., Chatelain, M., Dubiec, A., & Szulkin, M. (2021). Growing in the city: Urban evolutionary ecology of avian growth rates. *Evolutionary Applications*, 14, 69–84.
- Cosentino, B. J., Vanek, J. P., & Gibbs, J. P. (2023). Rural selection drives the evolution of an urban-rural cline in coat color in gray squirrels. *Ecology and Evolution*, 13, 17.
- Cronin, A. D., Smit, J. A. H., Munoz, M. I., Poirier, A., Moran, P. A., Jerem, P., & Halfwerk, W. (2022). A comprehensive overview of the effects of urbanisation on sexual selection and sexual traits. *Biological Reviews*, 97, 1325–1345.
- Crow, J. F. (1958). Some possibilities for measuring selection intensities in man. *American Anthropologist*, 60, 1–13.
- Culina, A., Adriaensen, F., Bailey, L. D., Burgess, M. D., Charmantier, A., Cole, E. F., Eeva, T., Matthysen, E., Nater, C. R., Sheldon, B. C., Sauther, B.-E., Vriend, S. J. G., Zajkova, Z., Adamik, P., Aplin, L. M., Angulo, E., Artemyev, A., Barba, E., Barisic, S., ... Visser, M. E. (2021). Connecting the data landscape of long-term ecological studies: The SPI-birds data hub. *Journal of Animal Ecology*, 90, 2147–2160.
- Darimont, C. T., Carlson, S. M., Kinnison, M. T., Paquet, P. C., Reimchen, T. E., & Wilms, C. C. (2009). Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 952–954.
- de Villemereuil, P. (2018). Quantitative genetic methods depending on the nature of the phenotypic trait. *Annals of the New York Academy of Sciences*, 1422, 29–47.
- de Villemereuil, P., Charmantier, A., Arlt, D., Bize, P., Brekke, P., Brouwer, L., Cockburn, A., Cote, S. D., Dobson, F. S., Evans, S. R., Festa-Bianchet, M., Gamelon, M., Hamel, S., Hegelbach, J., Jerstad, K., Kempnaers, B., Kruuk, L. E. B., Kumpula, J., Kvalnes, T., ... Chevin, L.-M. (2020). Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 31969–31978.
- de Villemereuil, P., Schielzeth, H., Nakagawa, S., & Morrissey, M. (2016). General methods for evolutionary quantitative genetic inference from generalized mixed models. *Genetics*, 204, 1281–1294.
- Diamond, S. E., & Martin, R. A. (2021). Evolution in cities. *Annual Review of Ecology, Evolution, and Systematics*, 52, 519–540.
- Dingemans, N. J., Araya-Ajoy, Y. G., & Westneat, D. F. (2021). Most published selection gradients are underestimated: Why this is and how to fix it. *Evolution*, 75, 806–818.
- Donihue, C. M., & Lambert, M. R. (2015). Adaptive evolution in urban ecosystems. *Ambio*, 44, 194–203.

- Dowling, J. L., Luther, D. A., & Marra, P. P. (2012). Comparative effects of urban development and anthropogenic noise on bird songs. *Behavioral Ecology*, 23, 201–209.
- Driscoll, C. A., Macdonald, D. W., & O'Brien, S. J. (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 9971–9978.
- Eanes, W. F. (1999). Analysis of selection on enzyme polymorphisms. *Annual Review of Ecology and Systematics*, 30, 301–326.
- Eisenhauer, J. G. (2021). Meta-analysis and mega-analysis: A simple introduction. *Teaching Statistics*, 43, 21–27.
- Foll, M., Shim, H., & Jensen, J. D. (2015). WFABC: A Wright-Fisher ABC-based approach for inferring effective population sizes and selection coefficients from time-sampled data. *Molecular Ecology Resources*, 15, 87–98.
- Franklin, O. D., & Morrissey, M. B. (2017). Inference of selection gradients using performance measures as fitness proxies. *Methods in Ecology and Evolution*, 8, 663–677.
- Fugere, V., & Hendry, A. P. (2018). Human influences on the strength of phenotypic selection. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 10070–10075.
- Gamelon, M., Tufto, J., Nilsson, A. L. K., Jerstad, K., Rostad, O. W., Stenseth, N. C., & Sæther, B. E. (2018). Environmental drivers of varying selective optima in a small passerine: A multivariate, multi-episodic approach. *Evolution*, 72, 2325–2342.
- Gorton, A. J., Moeller, D. A., & Tiffin, P. (2018). Little plant, big city: A test of adaptation to urban environments in common ragweed (*Ambrosia artemisiifolia*). *Proceedings of the Biological Sciences*, 285, 20180968.
- Grafen, A. (1988). On the uses of data on lifetime reproductive success. In T. Clutton-Brock (Ed.), *Reproductive success* (pp. 454–471). University of Chicago Press.
- Gregoire, A., Preault, M., Cezilly, F., Wood, M. J., Pradel, R., & Faivre, B. (2004). Stabilizing natural selection on the early expression of a secondary sexual trait in a passerine bird. *Journal of Evolutionary Biology*, 17, 1152–1156.
- Gregory, T. R. (2009). Artificial selection and domestication: Modern lessons from Darwin's enduring analogy. *Evolution: Education and Outreach*, 2, 5–27.
- Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J. G., Bai, X. M., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, 319, 756–760.
- Hadfield, J. D. (2008). Estimating evolutionary parameters when viability selection is operating. *Proceedings of the Royal Society B: Biological Sciences*, 275, 723–734.
- Hadfield, J. D., & Thomson, C. E. (2017). Interpreting selection when individuals interact. *Methods in Ecology and Evolution*, 8, 688–699.
- Harris, S. E., & Munshi-South, J. (2017). Signatures of positive selection and local adaptation to urbanization in white-footed mice (*Peromyscus leucopus*). *Molecular Ecology*, 26, 6336–6350.
- Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, 17, 20–29.
- Hendry, A. P., Gotanda, K. M., & Svensson, E. I. (2017). Human influences on evolution, and the ecological and societal consequences. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 372, 20160028.
- Henshaw, J. M., Morrissey, M. B., & Jones, A. G. (2020). Quantifying the causal pathways contributing to natural selection. *Evolution*, 74, 2560–2574.
- Henshaw, J. M., & Zemel, Y. (2017). A unified measure of linear and nonlinear selection on quantitative traits. *Methods in Ecology and Evolution*, 8, 604–614.
- Hereford, J., Hansen, T. F., & Houle, D. (2004). Comparing strengths of directional selection: How strong is strong? *Evolution*, 58, 2133–2143.
- Hersch, E. I., & Phillips, P. C. (2004). Power and potential bias in field studies of natural selection. *Evolution*, 58, 479–485.
- Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hoang, A., Hill, C. E., Beerli, P., & Kingsolver, J. G. (2001). Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 9157–9160.
- Hohenlohe, P. A., Bassham, S., Etter, P. D., Stiffler, N., Johnson, E. A., & Cresko, W. A. (2010). Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *PLoS Genetics*, 6, e1000862.
- Houle, C., Pelletier, F., Bélisle, M., & Garant, D. (2020). Impacts of environmental heterogeneity on natural selection in a wild bird population\*. *Evolution*, 74, 1142–1154.
- Irwin, R. E., Warren, P. S., & Adler, L. S. (2018). Phenotypic selection on floral traits in an urban landscape. *Proceedings of the Biological Sciences*, 285. <https://doi.org/10.1098/rspb.2018.1239>
- Janas, K., Gudowska, A., & Drobniak, S. M. (2024). Avian colouration in a polluted world: A meta-analysis. *Biological Reviews*, 99, 1261–1277.
- Janzen, F. J., & Stern, H. S. (1998). Logistic regression for empirical studies of multivariate selection. *Evolution*, 52, 1564–1571.
- Jarvi, T., & Bakken, M. (1984). The function of the variation in the breast stripe of the great tit (*Parus major*). *Animal Behaviour*, 32, 590–596.
- Johnson, M. T. J., & Munshi-South, J. (2017). Evolution of life in urban environments. *Science*, 358, eaam8327.
- Johnson, M. T. J., Prashad, C. M., Lavoignat, M., & Saini, H. S. (2018). Contrasting the effects of natural selection, genetic drift and gene flow on urban evolution in white clover (*Trifolium repens*). *Proceedings of the Royal Society B: Biological Sciences*, 285, 20181019.
- Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, 7, 1225–1241.
- Kingsolver, J. G., Diamond, S. E., Siepielski, A. M., & Carlson, S. M. (2012). Synthetic analyses of phenotypic selection in natural populations: Lessons, limitations and future directions. *Evolutionary Ecology*, 26, 1101–1118.
- Kopp, M., & Matuszewski, S. (2014). Rapid evolution of quantitative traits: Theoretical perspectives. *Evolutionary Applications*, 7, 169–191.
- Kruuk, L. E. B., Merila, J., & Sheldon, B. C. (2003). When environmental variation short-circuits natural selection. *Trends in Ecology & Evolution*, 18, 207–209.
- Lambert, M. R., Brans, K. I., Des Roches, S., Donihue, C. M., & Diamond, S. E. (2021). Adaptive evolution in citites: Progress and misconceptions. *Trends in Ecology & Evolution*, 36, 239–257.
- Lambrecht, S. C., Mahieu, S., & Cheptou, P. O. (2016). Natural selection on plant physiological traits in an urban environment. *Acta Oecologica-International Journal of Ecology*, 77, 67–74.
- Lande, R. (1982). A quantitative genetic theory of life-history evolution. *Ecology*, 63, 607–615.
- Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, 37, 1210–1226.
- Linnen, C. R., & Hoekstra, H. E. (2009). Measuring natural selection on genotypes and phenotypes in the wild. *Cold Spring Harbor Symposia on Quantitative Biology*, 74, 155–168.
- MacColl, A. D. C. (2011). The ecological causes of evolution. *Trends in Ecology & Evolution*, 26, 514–522.
- Macintyre, H. L., Heaviside, C., Cai, X. M., & Phalkey, R. (2021). The winter urban heat Island: Impacts on cold-related mortality in a highly urbanized European region for present and future climate. *Environment International*, 154, 9.
- Manel, S., Perrier, C., Pralong, M., Abi-Rached, L., Paganini, J., Pontarotti, P., & Aurelle, D. (2016). Genomic resources and their influence on the detection of the signal of positive selection in genome scans. *Molecular Ecology*, 25, 170–184.
- Marrot, P., Garant, D., & Charmantier, A. (2015). Spatial autocorrelation in fitness affects the estimation of natural selection in the wild. *Methods in Ecology and Evolution*, 6, 1474–1483.

- Matz, M. V. (2018). Fantastic beasts and how to sequence them: Ecological genomics for obscure model organisms. *Trends in Genetics*, *34*, 121–132.
- Mitchell-Olds, T., & Shaw, R. G. (1987). Regression analysis of natural selection: Statistical inference and biological interpretation. *Evolution*, *41*, 1149–1161.
- Mittell, E. A., & Morrissey, M. B. (2024). The missing fraction problem as an episodes of selection problem. *Evolution*, *78*, 601–611.
- Morrissey, M. B. (2014a). In search of the best methods for multivariate selection analysis. *Methods in Ecology and Evolution*, *5*, 1095–1109.
- Morrissey, M. B. (2014b). Selection and evolution of causally covarying traits. *Evolution*, *68*, 1748–1761.
- Morrissey, M. B. (2016). Meta-analysis of magnitudes, differences and variation in evolutionary parameters. *Journal of Evolutionary Biology*, *29*, 1882–1904.
- Morrissey, M. B., & Goudie, I. B. J. (2022). Analytical results for directional and quadratic selection gradients for log-linear models of fitness functions. *Evolution*, *76*, 1378–1390.
- Morrissey, M. B., & Hadfield, J. D. (2012). Directional selection in temporally replicated studies is remarkably consistent. *Evolution*, *66*, 435–442.
- Morrissey, M. B., & Henshaw, J. M. (2022). Phenotypic selection analysis and confounding environmental variables. *bioRxiv*, 2022.2006.2015.496257. <https://doi.org/10.1101/2022.06.15.496257>
- Morrissey, M. B., Kruuk, L. E. B., & Wilson, A. J. (2010). The danger of applying the breeder's equation in observational studies of natural populations. *Journal of Evolutionary Biology*, *23*, 2277–2288.
- Morrissey, M. B., & Ruxton, G. D. (2018). Multiple regression is not multiple regressions: The meaning of multiple regression and the non-problem of collinearity. *Philosophy, Theory, and Practice in Biology*, *10*. <https://doi.org/10.3998/ptpbio.16039257.0010.003>
- Morrissey, M. B., & Sakrejda, K. (2013). Unification of regression-based methods for the analysis of natural selection. *Evolution*, *67*, 2094–2100.
- Nicolaus, M., Piault, R., Ubels, R., Tinbergen, J. M., & Dingemanse, N. J. (2016). The correlation between coloration and exploration behaviour varies across hierarchical levels in a wild passerine bird. *Journal of Evolutionary Biology*, *29*, 1780–1792.
- Nielsen, R. (2005). Molecular signatures of natural selection. *Annual Review of Genetics*, *39*, 197–218.
- Otto, S. P. (2018). Adaptation, speciation and extinction in the Anthropocene. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 9.
- Palacio, F. X., & Ordano, M. (2023). Urbanization shapes phenotypic selection of fruit traits in a seed-dispersal mutualism. *Evolution*, *77*, 1769–1779.
- Palumbi, S. R. (2001). Evolution—Humans as the world's greatest evolutionary force. *Science*, *293*, 1786–1790.
- Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S., & Coulson, T. (2007). The evolutionary demography of ecological change: Linking trait variation and population growth. *Science*, *315*, 1571–1574.
- Pelletier, F., & Coltman, D. W. (2018). Will human influences on evolutionary dynamics in the wild pervade the Anthropocene? *BMC Biology*, *16*, 10.
- Pick, J. L., Lemon, H. E., Thomson, C. E., & Hadfield, J. D. (2022). Decomposing phenotypic skew and its effects on the predicted response to strong selection. *Nature Ecology & Evolution*, *6*, 774–785.
- Pinsky, M. L., Eikeset, A. M., Helmersen, C., Bradbury, I. R., Bentzen, P., Morris, C., Gondek-Wyrozemska, A. T., Baalsrud, H. T., Briec, M. S. O., Kjesbu, O. S., Godiksen, J. A., Barth, J. M. I., Matschiner, M., Stenseth, N. C., Jakobsen, K. S., Jentoft, S., & Star, B. (2021). Genomic stability through time despite decades of exploitation in cod on both sides of the Atlantic. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, 6.
- Price, G. R. (1970). Selection and covariance. *Nature*, *227*, 520–521.
- Price, T. D., Yeh, P. J., & Harr, B. (2008). Phenotypic plasticity and the evolution of a socially selected trait following colonization of a novel environment. *The American Naturalist*, *172*, S49–S62.
- Rausser, M. D. (1992). The measurement of selection on quantitative traits: Biases due to environmental covariances between traits and fitness. *Evolution*, *46*, 616–626.
- Reed, T. E., Visser, M. E., & Waples, R. S. (2023). The opportunity for selection: A slippery concept in ecology and evolution. *Journal of Animal Ecology*, *92*, 7–15.
- Riyahi, S., Björklund, M., Mateos-Gonzalez, F., & Senar, J. C. (2017). Personality and urbanization: Behavioural traits and DRD4 SNP830 polymorphisms in great tits in Barcelona city. *Journal of Ethology*, *35*, 101–108.
- Rodewald, A. D., & Arcese, P. (2017). Reproductive contributions of cardinals are consistent with a hypothesis of relaxed selection in urban landscapes. *Frontiers in Ecology and Evolution*, *5*, 77. <https://doi.org/10.3389/fevo.2017.00077>
- Rodewald, A. D., Shustack, D. P., & Jones, T. M. (2011). Dynamic selective environments and evolutionary traps in human-dominated landscapes. *Ecology*, *92*, 1781–1788.
- Ryder, T. B., Fleischer, R. C., Shriver, W. G., & Marra, P. P. (2012). The ecological–evolutionary interplay: Density-dependent sexual selection in a migratory songbird. *Ecology and Evolution*, *2*, 976–987.
- Salmón, P., López-Idiáquez, D., Capilla-Lasheras, P., Pérez-Tris, J., Isaksson, C., & Watson, H. (2023). Urbanisation impacts plumage colouration in a songbird across Europe: Evidence from a correlational, experimental and meta-analytical approach. *Journal of Animal Ecology*, *92*, 1924–1936.
- Santangelo, J. S., Ness, R. W., Cohan, B., Fitzpatrick, C. R., Innes, S. G., Koch, S., Miles, L. S., Munim, S., Peres-Neto, P. R., Prashad, C., Tong, A. T., Aguirre, W. E., Akinwole, P. O., Alberti, M., Alvarez, J., Anderson, J. T., Anderson, J. J., Ando, Y., Andrew, N. R., ... Johnson, M. T. J. (2022). Global urban environmental change drives adaptation in white clover. *Science*, *375*, 1275–1281.
- Scheiner, S. M., Mitchell, R. J., & Callahan, H. S. (2000). Using path analysis to measure natural selection. *Journal of Evolutionary Biology*, *13*, 423–433.
- Schluter, D. (1988). Estimating the form of natural selection on a quantitative trait. *Evolution*, *42*, 849–861.
- Senar, J. C., Conroy, M. J., Quesada, J., & Mateos-Gonzalez, F. (2014). Selection based on the size of the black tie of the great tit may be reversed in urban habitats. *Ecology and Evolution*, *4*, 2625–2632.
- Seress, G., Hammer, T., Bokony, V., Vincze, E., Preiszner, B., Pipoly, I., Sinkovics, C., Evans, K. L., & Liker, A. (2018). Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecological Applications*, *28*, 1143–1156.
- Shaw, R. G., & Geyer, C. J. (2010). Inferring fitness landscapes. *Evolution*, *64*, 2510–2520.
- Siepielski, A. M., DiBattista, J. D., & Carlson, S. M. (2009). It's about time: The temporal dynamics of phenotypic selection in the wild. *Ecology Letters*, *12*, 1261–1276.
- Slabbekoorn, H., & den Boer-Visser, A. (2006). Cities change the songs of birds. *Current Biology*, *16*, 2326–2331.
- Sol, D., Jovani, R., & Torres, J. (2003). Parasite mediated mortality and host immune response explain age-related differences in blood parasitism in birds. *Oecologia*, *135*, 542–547.
- Spear, M. M., Levi, S. J., Etterson, J. R., & Gross, B. L. (2023). Resurrecting urban sunflowers: Phenotypic and molecular changes between antecedent and modern populations separated by 36 years. *Molecular Ecology*, *32*, 5241–5259.
- Stern, A. J., Wilton, P. R., & Nielsen, R. (2019). An approximate full-likelihood method for inferring selection and allele frequency trajectories from DNA sequence data. *PLoS Genetics*, *15*, 32.
- Stinchcombe, J. R., Agrawal, A. F., Hohenlohe, P. A., Arnold, S. J., & Blows, M. W. (2008). Estimating nonlinear selection gradients using

- quadratic regression coefficients: Double or nothing? *Evolution*, 62, 2435–2440.
- Stinchcombe, J. R., Kelley, J. L., & Conner, J. K. (2017). How to measure natural selection. *Methods in Ecology and Evolution*, 8, 660–662.
- Stinchcombe, J. R., Simonsen, A. K., & Blows, M. W. (2014). Estimating uncertainty in multivariate responses to selection. *Evolution*, 68, 1188–1196.
- Svensson, E. I. (2023). Phenotypic selection in natural populations: What have we learned in 40 years? *Evolution*, 77, 1493–1504.
- Szulkin, M., Garroway, C. J., Corsini, M., Kotarba, A. Z., & Dominoni, D. (2020). How to quantify urbanization when testing for urban evolution? In M. Szulkin, J. Munshi-South, & A. Charmantier (Eds.), *Urban evolutionary biology* (pp. 13–35). Oxford University Press.
- Szulkin, M., Munshi-South, J., & Charmantier, A. (2020). *Urban evolutionary biology*. Oxford University Press.
- Theodorou, P., Radzevičiūtė, R., Kahnt, B., Soro, A., Grosse, I., & Paxton, R. J. (2018). Genome-wide single nucleotide polymorphism scan suggests adaptation to urbanization in an important pollinator, the red-tailed bumblebee (*Bombus lapidarius* L.). *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172806.
- Thompson, K. A., Rieseberg, L. H., & Schluter, D. (2018). Speciation and the city. *Trends in Ecology & Evolution*, 33, 815–826.
- Thompson, R. (2008). Estimation of quantitative genetic parameters. *Proceedings of the Royal Society B: Biological Sciences*, 275, 679–686.
- Thurman, T. J., & Barrett, R. D. H. (2016). The genetic consequences of selection in natural populations. *Molecular Ecology*, 25, 1429–1448.
- Tüzün, N., Op de Beeck, L., Brans, K. I., Janssens, L., & Stoks, R. (2017). Microgeographic differentiation in thermal performance curves between rural and urban populations of an aquatic insect. *Evolutionary Applications*, 10, 1067–1075.
- United Nations, D.o.E.a.S.A., Population Division. (2019). *World urbanization prospects: The 2018 revision (ST/ESA/SER.A/420)*. United Nations.
- Verrelli, B. C., Alberti, M., Des Roches, S., Harris, N. C., Hendry, A. P., Johnson, M. T. J., Savage, A. M., Charmantier, A., Gotanda, K. M., Govaert, L., Miles, L. S., Rivkin, L. R., Winchell, K. M., Brans, K. I., Correa, C., Diamond, S. E., Fitzhugh, B., Grimm, N. B., Hughes, S., ... Ziter, C. (2022). A global horizon scan for urban evolutionary ecology. *Trends in Ecology & Evolution*, 37, 1006–1019.
- Vitalis, R., Gautier, M., Dawson, K. J., & Beaumont, M. A. (2014). Detecting and measuring selection from gene frequency data. *Genetics*, 196, 799–817.
- Wade, M. J., & Kalisz, S. (1990). The causes of natural selection. *Evolution*, 44, 1947–1955.
- Walden, N., Lucek, K., & Willi, Y. (2020). Lineage-specific adaptation to climate involves flowering time in North American *Arabidopsis lyrata*. *Molecular Ecology*, 29, 1436–1451.
- Walsh, B., & Lynch, M. (2018). *Evolution and selection of quantitative traits*. Oxford University Press.
- Waters, C. N., Zalasiewicz, J., Summerhayes, C., Barnosky, A. D., Poirier, C., Galuszka, A., Cearreta, A., Edgeworth, M., Ellis, E. C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J. R., Richter, D. D., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., ... Wolfe, A. P. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, 351, aad2622.
- Whitehead, A., Pilcher, W., Champlin, D., & Nacci, D. (2012). Common mechanism underlies repeated evolution of extreme pollution tolerance. *Proceedings of the Royal Society B: Biological Sciences*, 279, 427–433.
- Wilkinson, M. D., Dumontier, M., Aalbersberg, I. J., Appleton, G., Axton, M., Baak, A., Blomberg, N., Boiten, J.-W., da Silva Santos, L. B., Bourne, P. E., Bouwman, J., Brookes, A. J., Clark, T., Crosas, M., Dillo, I., Dumon, O., Edmunds, S., Evelo, C. T., Finkers, R., ... Mons, B. (2016). The FAIR guiding principles for scientific data management and stewardship. *Scientific Data*, 3, 160018.
- Winchell, K. M., Aviles-Rodriguez, K. J., Carlen, E. J., Miles, L. S., Charmantier, A., De Leon, L. F., Gotanda, K. M., Rivkin, L. R., Szulkin, M., & Verrelli, B. C. (2022). Moving past the challenges and misconceptions in urban adaptation research. *Ecology and Evolution*, 12, 13.
- Wood, W. E., & Yezerinac, S. M. (2006). Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk*, 123, 650–659.
- Wood, Z. T., Palkovacs, E. P., Olsen, B. J., & Kinnison, M. T. (2021). The importance of eco-evolutionary potential in the Anthropocene. *BioScience*, 71, 805–819.
- Yang, J. C., & Bou-Zeid, E. (2018). Should cities embrace their heat islands as shields from extreme cold? *Journal of Applied Meteorology and Climatology*, 57, 1309–1320.
- Yeaman, S. (2015). Local adaptation by alleles of small effect. *The American Naturalist*, 186, S74–S89.
- Yeaman, S. (2022). Evolution of polygenic traits under global vs local adaptation. *Genetics*, 220, iyab134.
- Yeh, P. J., & Price, T. D. (2004). Adaptive phenotypic plasticity and the successful colonization of a novel environment. *The American Naturalist*, 164, 531–542.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1:** Raw output of the 439 hits resulting from a Google Scholar search conducted on 15/01/2024, for studies citing Lande & Arnold's seminal paper published in 1983, and including the search terms: urban\*, city\*, town\*, or metro\*.

**Table S2:** Search terms for Web of Science search described in Section 3.2.1.

**Table S3:** Estimates of linear selection differentials and gradients from studies listed in Table 1.

**Table S4:** Full list of 383 (deduplicated) articles resulting from the genomic Web of Science searches described in Table S2 and conducted on 08/11/2023.

**Table S5:** List of studies providing urban genomic signatures of selection from literature search detailed in Table S2.

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