Urban Signatures of Phenotypic Change: Emerging Patterns, Mechanisms, and Novel Hypotheses

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Humans challenge the phenotypic, genetic and cultural makeup of species by affecting the fitness landscapes on which they evolve. Recent studies show that cities might play a major role in contemporary evolution by accelerating phenotypic changes in wildlife, including animals, plants, fungi, and other organisms. Many studies of eco-evolutionary change have focused on anthropogenic drivers, but none of these studies have specifically examined the role that urbanization plays in eco-evolution or explicitly examined its mechanisms. This paper presents new evidence on the mechanisms linking urban development patterns to rapid evolutionary changes for species that play important functional roles in communities and ecosystems. Through a meta-analysis of experimental and observational studies reporting more than 1600 phenotypic changes in species across multiple regions, we ask whether we can discriminate an urban signature of phenotypic change beyond the established natural baselines and other anthropogenic signals. We then assess the relative impact of five types of urban disturbances including habitat modifications, biotic interactions, habitat heterogeneity, novel disturbances, and social interactions. Our study shows a clear urban signal; rates of phenotypic change are greater in urbanizing systems compared to natural and non-urban anthropogenic systems. By explicitly linking urban development to traits that affect ecosystem function, we can map potential eco-evolutionary implications of emerging patterns of urban agglomerations and uncover new insights for maintaining key ecosystem functions upon which the sustainability of human wellbeing depends.

Introduction

Emerging evidence of phenotypic change on contemporary time-scales challenges the assumption that evolution only occurs over hundreds or thousands of years. Anthropogenic changes in ecological conditions can drive evolutionary change in species traits that can alter ecosystem function (1–3). However, the reciprocal and simultaneous outcomes of such interactions have only begun to emerge (4). Despite increasing evidence that humans are major drivers of micro-evolution, the role of human activities in such dynamics is still unclear. Might human-driven evolution lead to ecosystem change with consequences for human wellbeing within contemporary time-scales (5, 6)?

To address this question, human-driven phenotypic change must be considered in the context of global rapid urbanization. In 1950, 30 percent of the world’s population lived in urban settlements (7). By 2014, that figure had risen to 54 percent, and by 2050 it is expected to reach 66 percent (7). By 2030, urban land cover is forecast to increase by 1.2 million km², nearly tripling the global urban land area of 2000 and potentially driving significant biodiversity loss (8). Urbanization drives systemic changes to socio-ecological systems by accelerating rates of interactions among people, multiplying connections among distant places, and expanding the spatial scales and ecological consequences of human activities to global levels (9).

A critical question for sustainability is whether, on an increasingly urbanized planet, the expansion and patterns of urban environments accelerate the evolution of ecologically relevant traits with potential impacts on urban populations via basic ecosystem services such as food production, carbon sequestration, and human health (e.g. infectious diseases). In cities, subtle and perhaps not so subtle eco-evolutionary changes are occurring at an unprecedented pace. Humans challenge the phenotypic, genetic, and cultural makeup of species on the planet by changing the fitness landscapes on which they evolve. Examples of contemporary evolution (sometimes called rapid evolution) associated with urbanization have been documented for many species (1, 5, 6, 10).

This paper examines the mechanisms linking urban development patterns to contemporary evolutionary changes. Through a meta-analysis of experimental and observational studies that report >1600 phenotypic changes in many species of birds, fish, arthropods, mammals, plants, and algae across multiple regions, we investigated the emergence of distinct signatures of urban-driven evolutionary change. We hypothesize that shifts in the physical and socio-economic structure and function of large urban complexes can drive rapid evolution on many species that play important roles in communities and ecosystems. Thus, urbanization-driven phenotypic change may, in turn, impact critical aspects of ecosystem function.

We ask two questions:

[1] Is there evidence of an urban signature of phenotypic change beyond the established natural and anthropogenic signals, accelerating rates of phenotypic change in species across multiple regions? [2] What are the relative impacts of five different types of urban disturbance: habitat modification, biotic interaction, heterogeneity, novel disturbance, and social interaction?

Our hypothesis is grounded in the growing evidence that urbanization is a major driver of contemporary evolution through several mechanisms that operate simultaneously across multiple scales. Urban development changes habitat structure (i.e., loss of forest cover and connectivity) and processes (i.e., biogeochemical and nutrient cycling), and it also modifies biotic interactions (i.e., predation) (6). Humans in cities also mediate eco-evolutionary interactions by introducing novel disturbances and altering habitat heterogeneity. Urban environments can facilitate hybridization by bringing together species that were previously reproductively isolated (11). They can also isolate populations through habitat fragmentation (12). In addition to changes in the physical

Significance Statement

Eco-evolutionary feedbacks on contemporary timescales were hypothesized over half a century ago, but only recently has evidence begun to emerge. The role that human activity plays in such dynamics is still unclear. Through a meta-analysis of experimental and observational studies that report >1600 phenotypic changes in species across regions and ecosystem types, we examine the evidence that the rate of phenotypic change has an urban signature. Our findings indicate greater phenotypic change in urbanizing systems compared to natural and non-urban anthropogenic systems. By explicitly linking urban development to trait changes that might affect ecosystem function, we provide insights into the potential eco-evolutionary implications for maintaining ecosystem function and the sustainability of human wellbeing.
template, humans in cities modify the availability of resources and their
variability over time, buffering their effects on community structure (12).
Complex interactions resulting from changes in habitat and biotic
interactions coupled with emerging spatial and temporal patterns of
resource availability might produce new evolutionary dynamics and
feedbacks. Furthermore, what makes cities unique is the pace of change
associated with increasing social interactions that amplify the direct and
indirect impacts of human agency, both locally and in distant places
(telecoupling). Understanding how urban-driven contemporary evolution
affects ecosystem functions and services will provide new insights for
maintaining biodiversity and achieving global urban sustainability.

Results
We discriminated the emergence of distinct signatures of
urbanization by statistically modeling an organism’s phenotypic change
as a function of urban disturbances, urban proximity, and other previously
identified variables potentially affecting phenotypic change. Using
generalized linear mixed-effect models (GLMM), in an information-
theoretic framework to enforce parsimony and acknowledge model
uncertainty, we analyzed a modified and geo-referenced version of a
database of rates of phenotypic change that has been developed over
two decades (5, 13–17). After a series of quality filters, we retained for
analyses 89 suitable studies targeting 155 species, 175 study systems,
and >1600 rates of phenotypic change (Figure 1) (Supporting Information
SI, p.1-3).

Statistical models including urban variables out-performed models
lacking urban variables, while accounting for anthropogenic context and
other putatively important variables described below. Hendry et al. (2008)
(15) showed that organisms in an anthropogenic context (e.g., pollution,
overharvest) had higher rates of phenotypic change compared to those
in a natural context. It was unclear whether urban variables would add
explanatory power after statistically controlling for the effect of
anthropogenic context. Our results showed that urban variables provide
substantial additional information for explaining phenotypic change, thus
warranting further consideration (SI, p.5-9).

The multifarious effects of urban agglomerations occur across
multiple spatial scales (9). Hence, we evaluated the effects of
urbanization considering both variables determined by location relative to
urban agglomerations, and urban-driven processes regardless of
location. Urban predictor variables included Urban Disturbance
(categorical, 8 classes of urban-related mechanisms plus one reference
natural state), City Lights (ordinal, ranging from 0 to 1 – wildland to city),
Anthropogenic Biome (ordinal, ranging from 1 to 6 – dense settlements to
wildlands), and Urbanization (continuous, difference in Anthropogenic
Biome between years 1900 and 2000) (SI, p.4). Since some phenotypic
changes were measured from populations at two locations (see Design),
continuous and ordinal predictor variables were calculated both as mean
and delta (difference) between the two samples underlying a phenotypic
change. Overall, this analysis included six urban variables representing a
range of possible mechanisms, scales, and proxies of urban drivers of
phenotypic change (see Materials and Methods). We also included three
unrelated variables that may affect rates of phenotypic change (13–15):
(1) number of Generations (continuous, log-transformed), (2) whether the
phenotypic change was estimated from a longitudinal or cross-sectional
study Design (categorical, 2 classes – allochronic and synchronic), and
(3) whether the phenotypic change had a demonstrated genetic basis or
not (labeled GenPhen, categorical, 2 classes – genotypic and phenotypic). We refer to these three a priori variables (Generations,
Design, and GenPhen) as background variables.

We conducted exploratory multimodel ranking and inference based
on second-order Akaike Information Criteria (AICc) to evaluate the
relative ability of urban and background variables to statistically explain
the absolute magnitude of standardized phenotypic change, and to
assess effect sizes averaged over all possible models (18). A large model

![Image](https://earthobservatory.nasa.gov/Features/NightLights/page3.php)

Fig. 1. Global distribution of study systems of trait changes in wild populations. Symbols represent Urban Disturbances, wherein each study system is
categorized according to its primary driver of phenotypic trait change. White regions represent City Lights as interpreted by Zhou et al. (2015) (53).
Background of the Earth in 2012 from NASA: earthobservatory.nasa.gov/Features/NightLights/page3.php
set (512 models) was created by considering all combinations of the nine explanatory variables in the fixed part of the GLMM (see Materials and Methods, p. 10-15). The random part of all models was held constant, and included a random intercept per Study System to account for nested data structure, and a previously selected variance function that allowed the residual variance to scale with the expected response. Phenotypic change (square-rooted) was the response variable, measured as the absolute magnitude of phenotypic change standardized by character variation, a quantity known as Haldane numerator (19).

Discussion

Our results show a clear urban signal of phenotypic change and reveal variable effects of urban disturbance mechanisms. Urban Disturbance, Habitat modification, Novel disturbances, Heterogeneity, Introduction, and Expansion were prevalent (Figure 2). Model-averaged partial regression coefficients (incorporating model uncertainty) revealed several strong and many weak effects (Table 1). Among urban-related variables, phenotypic changes estimated from contrasts between urban vs. wild habitats (i.e., Δ City Lights) were higher than contrasts within either urban or wild habitats. Mean City Lights, however, did not show a significant effect. Urbanization, inferred from land-cover change during the last century (mean Urbanization, with negative scores representing urbanization) showed a trend with highest rates of phenotypic change in urbanizing locations. This trend was not supported by the effect of contemporary land cover (Anthrobiome). Urban Disturbance had many effects. For example, social interactions, novel disturbances and introduction of predators, prey, hosts, or competitors, were associated with relatively high phenotypic change. Some effects were counterintuitive, e.g., habitat modification was associated with relatively low phenotypic change. The effects of Urban Disturbance were further illustrated by multimodel predictions made while the effects of other variables were statistically held constant (Figure 3). The range of effects attributed to Urban Disturbance on multi-model predictions were substantial compared to those of different combinations of background variables (SI9).

Table 1: Model-averaged coefficients from the full model set revealed several strong and many weak effects.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Z-score</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.545</td>
<td>0.097</td>
<td>5.619</td>
<td>0.000***</td>
</tr>
<tr>
<td>Generations</td>
<td>0.032</td>
<td>0.015</td>
<td>2.22</td>
<td>0.026*</td>
</tr>
<tr>
<td>Design – Synchronic</td>
<td>0.034</td>
<td>0.065</td>
<td>0.528</td>
<td>0.597</td>
</tr>
<tr>
<td>GenPhen – Phenotypic</td>
<td>0.104</td>
<td>0.052</td>
<td>2.006</td>
<td>0.045*</td>
</tr>
<tr>
<td>Mean. City Lights</td>
<td>0.056</td>
<td>0.033</td>
<td>1.695</td>
<td>0.090</td>
</tr>
<tr>
<td>Δ City Lights</td>
<td>0.072</td>
<td>0.031</td>
<td>2.344</td>
<td>0.019*</td>
</tr>
<tr>
<td>Δ Anthrobiome</td>
<td>-0.009</td>
<td>0.008</td>
<td>1.141</td>
<td>0.254</td>
</tr>
<tr>
<td>Δ Anthrobiome</td>
<td>-0.002</td>
<td>0.009</td>
<td>0.216</td>
<td>0.829</td>
</tr>
<tr>
<td>Mean Urbanization</td>
<td>-0.014</td>
<td>0.008</td>
<td>1.799</td>
<td>0.072</td>
</tr>
<tr>
<td>U. Dist. – Hetero</td>
<td>0.019</td>
<td>0.097</td>
<td>0.200</td>
<td>0.841</td>
</tr>
<tr>
<td>U. Dist. – HabMod</td>
<td>-0.371</td>
<td>0.046</td>
<td>8.088</td>
<td>0.000***</td>
</tr>
<tr>
<td>U. Dist. – Novel</td>
<td>0.14</td>
<td>0.136</td>
<td>1.028</td>
<td>0.304</td>
</tr>
<tr>
<td>U. Dist. – Social</td>
<td>0.425</td>
<td>0.154</td>
<td>2.753</td>
<td>0.006**</td>
</tr>
<tr>
<td>U. Dist. – Int</td>
<td>0.077</td>
<td>0.073</td>
<td>1.061</td>
<td>0.289</td>
</tr>
<tr>
<td>U. Dist. – IntEco</td>
<td>0.345</td>
<td>0.126</td>
<td>2.738</td>
<td>0.006**</td>
</tr>
<tr>
<td>U. Dist. – ExpAint</td>
<td>0.005</td>
<td>0.09</td>
<td>0.059</td>
<td>0.953</td>
</tr>
</tbody>
</table>

Significance levels: P<0.001(***), P<0.01 (*), P<0.05 (**), P<0.1 (.)

Abbreviations: Urban disturbance (U. Dist.), habitat modification (HabMod), heterogeneity (Hetero), and subcategories of biotic interaction: introduction (Int), introduction of predator/prey/host/competition (IntEco), range expansion after introduction (ExpAint).

Figure 2. Representation of the AICc model-selection table. Rows represent models sorted by decreasing empirical support (row height represents model probability conditional on the full model set). Predictor variables were shaded if included in a model. Saturation corresponded to estimated variable relative importance. Note all high-ranked models contained urban (e.g., Urban Disturbance) and background variables (e.g., Generations). Models with little relative support were omitted for clarity (95% confidence set displayed).

Figure 3. Multi-model predictions for Urban Disturbance categories. Some categories were associated with relatively high phenotypic change (i.e., Social interactions and Introduction of predator/prey/host/competition) whereas others associated with background or even stable phenotypes (Habitat modification). Modelled, but not shown variables were held constant at means (continuous variables) or reference values (categorical variables).
Urban Disturbance Mechanisms

Urban Disturbance represents coupled mechanisms through which urban development affects natural processes and evolutionary dynamics. Models predict high three categories driving the urban signature: social interactions, novel disturbances, and biotic interactions, specifically the introduction of predators, prey, and competitors. Anthropogenic habitat modification was of lesser impact.

Habitat modification

Land cover conversion and loss of native habitat are major drivers of contemporary evolution. Surprisingly, habitat modification driven by anthropogenic change was not among the dominant drivers of higher phenotypic change relative to the Natural context, suggesting that, globally, natural drivers of contemporary evolution might have greater effects on phenotypic traits. In part, the effect of urban land cover on phenotypic change is captured by City Lights. Yet urban-driven land conversion affects species composition through subtle mechanisms not captured by City Lights, but captured by our Urban Disturbance variable.

For example, changes in climate, artificial lighting, and availability of food are primary drivers of change in the timing and duration of reproduction in some bird species (21). Changes in productivity—the rate at which energy flows through an ecosystem—might explain species diversity patterns along the urban-to-rural gradient, though studies have produced contradictory results. Changes in net primary production associated with urban land-cover change affect faunal and plant species richness (22).

Biotic Interactions

We determined that among subcategories of biotic interactions, introduction of predator, prey, host, or competition contributes to a higher rate of phenotypic change compared to range expansion after introduction or introduction alone. Urban development creates new opportunities and challenges for species competition and predation, both as exotic species are introduced and as invasive species migrate in, taking advantage of poorly integrated communities and patches in the urban setting. This might result in a colonization process, as more frequent introductions of exotic species translate into invasions (23). For example, along a 140km urban-to-rural environmental gradient originating in New York City, McDonnell et al. (1997) (24) found higher levels of earthworm biomass and abundance in urban forests compared to rural ones, likely because of introduced species. Urbanization also alters the way species distribute and interact (25). Marzluff (2005) (26) found that while diversity still emerges as the balance between extinction and colonization, species invasion plays a prominent role.

Heterogeneity

The results provide evidence that cities directly and indirectly affect species diversity by altering spatial and temporal habitat heterogeneity. Increasing evidence supports the hypothesis that urban regions amplify heterogeneity by the intensity and speed of human-biophysical and social interactions (26). Cities worldwide retain significant numbers of native species, but loss of functional heterogeneity driven by urbanization affects niche differentiation and species diversity (27). Furthermore, changes associated with urban land uses act as filters in urban species composition, and losses of native species drive the homogenization of ecological structures and functions (28). Habitat patches and their ecological communities are often isolated by a matrix of built environments. Fragmentation of natural patches due to urbanization affects the diversity, structure, and distribution of vegetation, and movement of organisms (29). Change in temporal microclimatic heterogeneity (e.g., heat islands) can extend the growing season in temperate cities, and droughts in desert urban areas (30).

Novel Disturbance

Novel disturbance emerges as a dominant driver of phenotypic change. Human-induced disturbances in urban environments maintain urban habitats at an early successional stage (31). Such novel disturbances alter resource availability, ecosystem productivity, and species diversity (31). Cardinale et al. (2006) (32) suggested two ways that disturbance can moderate relationships between biodiversity and ecosystem functioning: it can increase the chance that diversity generates unique system properties, and it can suppress the probability of ecological processes being controlled by a single taxon. Urbanization not only modifies existing disturbance regimes (e.g., fire and flood management); it also creates novel disturbances including disrupted dispersal pathways or stressors, eco-toxins and pollutants (33, 34). Examples of phenotypic changes in response to new toxins include earthworms' tolerance to metals (33) and changes in endocrine systems of fish and birds (34).

Social Interactions

Perhaps the most significant quality that distinguishes cities is their pace of change. Urbanization changes the dynamics of socio-ecological interactions by increasing interactions among people (35), between people and other species (36), and among distant places (9). Important properties of cities of all sizes (i.e., gross domestic product) increase, on average, faster than city population size (superlinearity). Increasing social interactions accelerate environmental changes and human impact on phenotypic traits via selective harvest (5).

Socio-economic shifts associated with urbanization can explain the emergence of a detectable urban signature of evolutionary change. This is also evident from the simultaneous effects of the Urban Disturbance and City Light variables. The urban extent, regardless of boundary definitions, only partially defines the extent of urban disturbances. City functions depend on highly interconnected infrastructures and on flows of material, energy, and information from both proximate regions (e.g., via hydroelectric dams) and distant ones (e.g., via trade and telecommunication). In urbanizing regions, distant human-natural interactions are currently more prevalent and faster (9), challenging the ability to disentangle urban vs. non-urban anthropogenic influences on phenotypic traits.

Linking urban evolutionary change to ecosystem function

By explicitly linking urban development to traits that affect ecosystem functions and services, we start to map the eco-evolutionary implications of urban-driven phenotypic trait changes and identify existing gaps in knowledge. The evolution of antibiotic resistance, pesticide resistance, host-pathogen co-evolution, and evolution in response to harvest and habitat change provide examples of the link between human-driven evolution and sustainability (51). Urban environments provide the context for many such interactions, bringing people in to contact with novel pathogens, accelerating the spread of genes that confer resistance, and generally selecting for traits that enhance the survival and reproduction of wild organisms within human-built environments. When this selection facilitates the survival of desirable species, it can have important benefits for biodiversity, human health, and ecosystem services. For example, evolution of Daphnia may help improve water quality in the face of cultural eutrophication (37). However, adaptation can also enable the survival and reproduction of species that reduce biodiversity and human wellbeing. For example, evolution of pesticide resistance in agriculture and antibiotic resistance in human medicine represent critical threats to food security and human (38, 39). Thus, evolution is instrumental to sustainability and should take on a prominent role in the future of sustainability science.

Table 2 identifies examples of traits for which there is evidence of evolutionary response to environmental changes driven by urbanization. The evolution of traits that control ecosystem processes could lead to significant changes in ecosystem functions (40). For example, primary productivity is associated with consumers' traits that regulate their demands for resources. Evolution in such traits can affect nutrient cycling and ultimately the magnitude and spatial distribution of primary production (4). Seed dispersers have a significant impact on plant diversity and their functional roles in urban ecosystems. A great diversity of organisms modify the physical structure of estuarine and coastal environments, particularly dune and marsh plants, mangroves, seagrasses, kelps, and infauna (41). Evolution in ecosystem-engineering traits has potential functional impacts on maintaining the stability and resilience (e.g., flood control) of coastal cities and the capacity of cities to adapt to climate change.
Table 2: Mapping urban-driven phenotypic trait change to ecosystem function. Documented phenotypic trait changes, urban drivers, and hypothesized eco-evolutionary feedback mechanisms.

<table>
<thead>
<tr>
<th>Urban Signatures</th>
<th>Phenotypic trait</th>
<th>Eco-evolutionary feedback</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Urban Disturbance</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Novel</td>
<td>Exposure to effluent and associated extreme heat from a steam-electric plant</td>
<td>Mean heat coma temperature (thermal tolerance) in freshwater snails (<em>Physa virgata</em>)</td>
<td></td>
</tr>
<tr>
<td>Habitat modification</td>
<td>Anthropic acidification (pollution) of lake habitats</td>
<td>Survival in acidic conditions in moor frogs (<em>Rana arvalis</em>)</td>
<td></td>
</tr>
<tr>
<td>Novel</td>
<td>Electricity pylons create novel habitats characterized by high levels of zinc</td>
<td>Zinc tolerance in plants: <em>Agrostis capillaris</em>, <em>Agrostis stolonifera</em>, etc.</td>
<td></td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>Hydrological connectivity altered via a fish ladder</td>
<td>Body size in brown trout (<em>Salmo trutta</em>)</td>
<td></td>
</tr>
<tr>
<td>Biotic interaction</td>
<td>Invasion of a molluskivorous crab (<em>Carcinus maenas</em>)</td>
<td>Shell thickness (mm) in periwinkle snail (<em>Littorina obtusa</em>)</td>
<td></td>
</tr>
<tr>
<td>Social Interaction</td>
<td>Long-term selective harvesting of a medicinal plant</td>
<td>Size of American ginseng plants (<em>Panax quinquefolius</em>)</td>
<td></td>
</tr>
<tr>
<td>Biotic interaction</td>
<td>Introduction (translocation) of animals to a predator-free island</td>
<td>Antipredator behavior in multiple species of marsupials</td>
<td></td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>Temporal heterogeneity in water availability (drought)</td>
<td>Flowering time in Field mustard (<em>Brassica rapa</em>)</td>
<td></td>
</tr>
<tr>
<td>Habitat modification</td>
<td>Global warming</td>
<td>Seasonal onset of reproduction in 65 species of migratory birds</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Biodiversity</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Eco-evolutionary feedback</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feedback mechanism</td>
<td></td>
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<td></td>
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</tbody>
</table>

**Conclusions**

Rapid urbanization poses new challenges for species—some will go extinct (at least locally) while others will adapt or relocate (50). Our paper asked whether we can detect signatures of eco-evolutionary change across taxa in urban ecosystems and determine the extent to which systemic changes to eco-socio-ecological systems associated with urban agglomerations may accelerate phenotypic change. We found a clear urban signal of phenotypic change, and greater phenotypic change in urbanizing systems compared to natural and non-urban anthropogenic systems. By explicitly linking urban development to heritable traits affecting ecosystem function, we can begin to map the eco-evolutionary implications of human-induced trait changes for Earth’s evolution.

We posit that urban-driven contemporary evolution will affect sustainability, from the level of the urban ecosystem to the planetary scale. We suggest that conservation biologists should pay increased attention to mechanisms by which the emergent human habitat influences population persistence (4). Such understanding will provide new insights for maintaining ecosystem function in the long term and can direct policy makers toward novel sustainability solutions (51).

**Materials and Methods**

We improved an existing database on rates of phenotypic change (5, 13–17). We added new data published up to August of 2015. Studies were surveyed by searching ISI Web of Science, Google Scholar, and cross-references, using ad hoc keywords (e.g., quantitative trait, evolutionary change, rapid evolution, eco-evolutionary, anthropogenic change, urban disturbances, and system stability). Studies were screened for eligibility (see Database filtering in SI), and, if selected, phenotypic rates were extracted (see Statistical analyses) and classified according to qualities of the study system including ecological and anthropogenic contexts (5). Each row corresponded to one phenotypic change rate estimate and associated contextual attributes including type of study: allochronic for longitudinal studies, or sychronic for cross-sectional studies comparing samples obtained synchronously from populations derived from a common ancestral population. Rates were classified according to if phenotypic change could be attributed to quantitative genetic effects (Genetic), or could not be distinguished from phenotypic plasticity (Phenotypic).

Generations was calculated as the number of years between population samples (or since population divergence, if Synchronic) divided by expected generation time.

The data set had a hierarchical structure, with variable numbers of phenotypic change estimates (from different morphological characters and or populations) within study systems, species, and taxa. Study system was defined as (a) population(s) of a species within a geographical region putatively exposed to similar environmental effects and high gene flow potential. Two important contextual variables were evaluated at the study-system level: whether study systems were regarded as evolving in an anthropogenic or a natural Context (15), and Urban disturbance (see next section).

**Urban Disturbance classification and geo-referencing**

We use the global urban area map at 1 km spatial resolution developed by Zhou et al. (2015) (52). The map is based on a cluster-based method to estimate optimal thresholds for mapping urban extent using DMSP/OLS NTL to account for regional variations in urban clusters, calibrated using high-resolution land cover data for the US and China in 2005 (53). The anthropogenic biome of all samples was based on the Anthropogenic Biomes geodataset for the year 2000 (54).

For samples in study systems in which the driver of evolutionary change is anthropogenic, we classify the Urban Disturbance as social interaction, biotic interaction (with subcategories for introduction, introduction of predator/prey/host/competition, and range expansion after introduction), habitat modification, heterogeneity, or novel disturbance (6) (See Urban disturbance classification in SI). Habitat modification represents changes in climate, modification of the landscape, or pollution. Biotic interactions stem from introductions, and are subcategorized depending on the study organism’s ecological role: introduced species vs. species in its native range responding to an introduction. Introduced species are further divided into species adapting in a new range following introduction vs. introduced species adapting following range expansion. Heterogeneity can refer to heterogeneity in space or time, e.g., pulsed disturbances from discharge of a geothermal plant (55). Novel disturbances require novel adaptations, e.g., rapid evolution of zinc tolerance (43). Social interactions refer to direct or intentional results of human agency, e.g., trophy hunting (56).

**Statistical analyses**

We used an information-theoretic approach to rank statistical models and conduct multimodel inference, based on AICc (57)(61, 23). AICc favors model fit (minimizing
deviance) while avoiding model overfitting (penalizing for the number of estimated parameters, K), and was the basis for enforcing the parsimony principle given our finite sample sizes (1663 rates nested in 175 Study systems). The statistical models were generalized linear mixed-effect models (GLMM). The response variable, phenotypic change (square-root transformed), was measured as the absolute magnitude of phenotypic change standardized by character variation (Haldane numerator; 19, as formulated in 13). The square-root transformation minimized patterns in adjusted residuals plots in preliminary analyses. Because the data had a hierarchical structure, study system was always modelled as a random effect, with combinations of background and urban variables (fixed effects): 

\[ \alpha = N(\mu, \sigma^2 \alpha) \]

\[ \alpha = \frac{\lambda - \lambda_1}{\lambda_1 - \lambda_2} \]

where the indexes \( i \) run from 1 to number of observations, and \( j \) run from 1 to number of study systems, \( H(\alpha) \) is the response variable (square-root of Haldane numerator), \( \alpha \) is normally distributed with mean \( \mu \) (overall intercept) and variance \( \sigma^2 \alpha \), allowing for varying intercepts per study system, \( \beta \) a vector of partial regression coefficients related to a matrix of explanatory variables \( X \), and \( \epsilon \), the residual error with variance \( \gamma \), which was modelled as follows:

\[ \gamma = 0.1494 \times (C + \text{fitted})^2 \]

where \( C \) is a constant by stratum (0.3233 for genetic; 0.1249 for phenotypic), and \( P \) an exponent of absolute fitted values by stratum (2.0754 for genetic; 1.2376 for phenotypic). Hence, the chosen residual variance increased exponentially with fitted values, and slightly more so in genetic than phenotypic rates (SI, p. 10-15).

We used exploratory multilevel inference to assess the relative importance of predictor variables (urban or not) for phenotypic change, and to make predictions about contrasting urban-related scenarios that considered information contained in all models. From 3 background plus 6 urban explanatory variables to form 512 models, including a null model (intercept only), and excluding interactions. All models were fitted through maximum likelihood (ML) in the R package nlme (58). Models were ranked according to decreasing values of AICc (59), and further evaluated using standard methods after re-fitting through REML estimation (60). Predictor variable relative importance was calculated by the sum of the Akaike weights of all models containing a particular predictor variable. Similarly, model-averaged partial regression coefficients were Akaike-weighted averages of coefficients from all models containing a particular term (18). Model ranking and inference was conducted in the R package MultinMA v1.15.6 (57) (SI, p.10-15).