

# Global urban signatures of phenotypic change in animal and plant populations

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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 ecoevolutionary change have focused on anthropogenic drivers, but none of these studies has specifically examined the role that urbanization plays in ecoevolution or explicitly examined its mechanisms. This paper presents 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 metaanalysis of experimental and observational studies reporting more than 1,600 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 with natural and nonurban anthropogenic systems. By explicitly linking urban development to traits that affect ecosystem function, we can map potential ecoevolutionary implications of emerging patterns of urban agglomerations and uncover insights for maintaining key ecosystem functions upon which the sustainability of human well-being depends.**

ecoevolution | urbanization | ecosystem function | sustainability | anthropocene

**E**merging evidence of phenotypic change on contemporary timescales 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 microevolution, the role of human activities in such dynamics is still unclear. Might human-driven evolution lead to ecosystem change with consequences for human well-being within contemporary timescales (5, 6)?

To address this question, human-driven phenotypic change must be considered in the context of global rapid urbanization. In 1950, 30% of the world's population lived in urban settlements (7). By 2014, that figure had risen to 54%, and by 2050 it is expected to reach 66% (7). By 2030, urban land cover is forecast to increase by 1.2 million km<sup>2</sup>, almost tripling the global urban land area of 2000 (8). Urbanization drives systemic changes to socioecological 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. In cities, ecoevolutionary 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 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 metaanalysis of experimental and observational studies that report >1,600 phenotypic changes in many species across multiple regions, we investigated the emergence of distinct signatures of urban-driven phenotypic change. We hypothesize that shifts in the physical and socioeconomic structure and function of large urban complexes can drive rapid evolution of 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 the following two questions: (i) 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? (ii) What are the relative impacts of five types of urban disturbance: habitat modification, biotic interaction, heterogeneity, novel disturbance, and social interaction?

## Significance

**Ecoevolutionary 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 metaanalysis of >1,600 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 with natural and nonurban anthropogenic systems. By explicitly linking urban development to trait changes that might affect ecosystem function, we provide insights into the potential ecoevolutionary implications for maintaining ecosystem function and the sustainability of human well-being.**

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Our hypothesis is grounded in the growing evidence that urbanization is a major driver of contemporary evolution. Urban development changes habitat structure (i.e., loss of forest cover and connectivity), processes (i.e., biogeochemical and nutrient cycling), and biotic interactions (i.e., predation) (6). Humans in cities mediate ecoevolutionary interactions by introducing novel disturbances and altering habitat heterogeneity. Urban environments can facilitate hybridization by reducing reproductive isolation (11). They can also isolate populations through habitat fragmentation (12). In addition to changes in the physical 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, in cities, the rapid pace of change associated with increasing social interactions amplifies the impacts of human agency, both locally and at a distance (telecoupling). Understanding how urban-driven contemporary evolution affects ecosystem functions will provide insights for maintaining biodiversity and achieving global urban sustainability.

## Results

We discriminated the emergence of distinct signatures of urbanization by statistically modeling phenotypic change as a function of urban disturbances, urban proximity, and other potentially relevant previously identified variables. Using generalized linear mixed-effect models (GLMMs), in an information-theoretic framework to enforce parsimony and acknowledge model uncertainty, we analyzed a modified and georeferenced 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 studies targeting 155 species, 175 study systems, and >1,600 rates of phenotypic change (Fig. 1) (*SI Appendix, Database Filtering*).

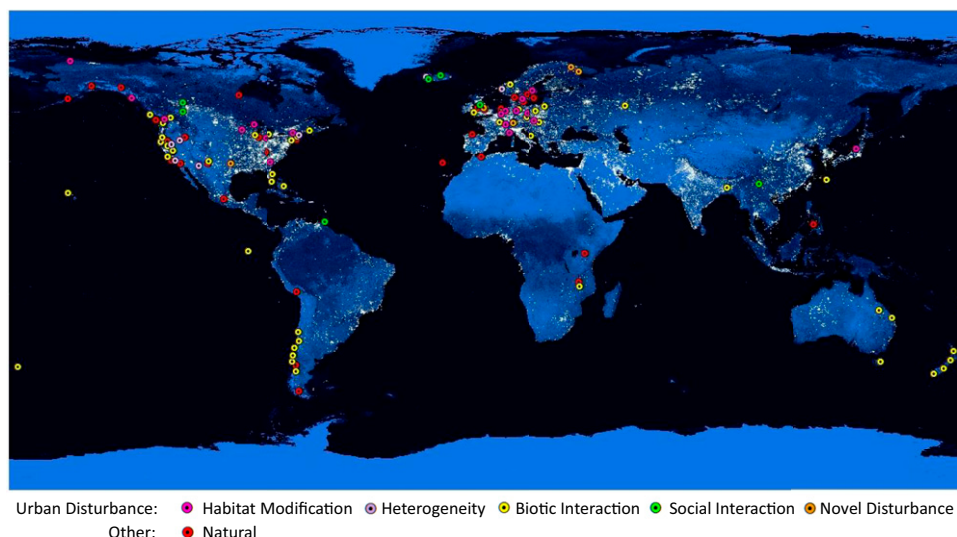
Statistical models including urban variables outperformed models lacking urban variables, while accounting for anthropogenic context and other putatively important variables described below. Hendry et al. (15) showed that organisms in an anthropogenic context (e.g., pollution, overharvest) had higher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

consideration (*SI Appendix, Gauging the Urban Signature Beyond the Anthropogenic Context*).

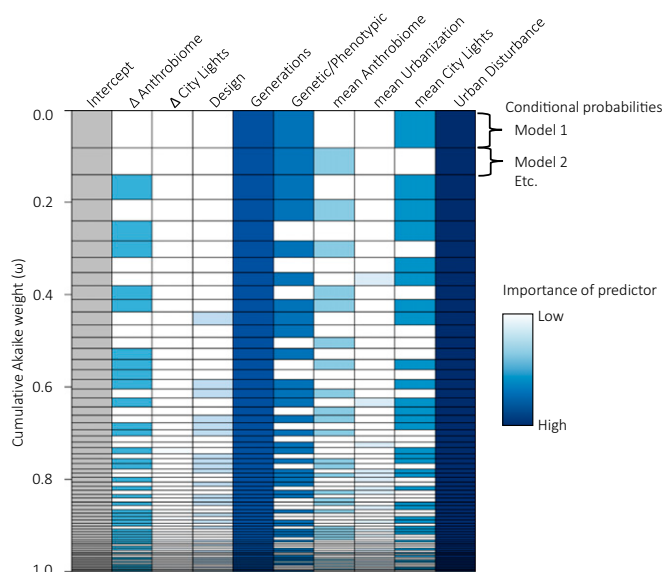
The multifarious effects of urban agglomerations occur across multiple spatial scales (9). Hence, we considered both variables determined by location relative to urban agglomerations and urban-driven processes regardless of location. Urban predictor variables included Urban Disturbance (categorical, seven 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 (difference in Anthropogenic Biome between years 1900 and 2000) (*SI Appendix, Urban Disturbance Classification*). Because 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. This analysis included six urban variables representing a range of possible mechanisms, scales, and proxies of urban drivers of phenotypic change (*Materials and Methods*). We also included three unrelated background variables that may affect phenotypic change (13–15): (i) number of Generations (continuous, log-transformed); (ii) whether the phenotypic change was estimated from a longitudinal or cross-sectional study Design (categorical, two classes—allochronic and synchronic); and (iii) whether the phenotypic change had a demonstrated genetic basis or not (labeled GenPhen, categorical, two classes—genotypic and phenotypic).

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 set (512 models) was created by considering all combinations of the nine explanatory variables in the fixed part of the GLMM (*Materials and Methods* and *SI Appendix, Materials and Methods—Statistical Analysis*). 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).

Top-ranked models consistently included urban variables. For example, the focal variables Urban Disturbance, City Lights, and Anthrobiome are prevalent in top-ranked models and in the 95% confidence set, whereas, among background variables, Generations



**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. Background of the Earth in 2012 from NASA: [earthobservatory.nasa.gov/Features/NightLights/page3.php](http://earthobservatory.nasa.gov/Features/NightLights/page3.php).



**Fig. 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).

and GenPhen were prevalent (Fig. 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.,  $\Delta$  City Lights) were higher than contrasts within either urban or wild habitats. Mean City Lights, however, showed only a marginally significant effect ( $P < 0.1$ ). 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 several effects. For example, social interactions, and introduction of predators, prey, hosts, or competitors, were associated with relatively high phenotypic change. Some effects were counterintuitive, for example, 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 (Fig. 3). The range of effects attributed to Urban Disturbance on multimodel predictions were substantial compared with those of different combinations of background variables (*SI Appendix, Database Filtering*).

## Discussion

Our results show a clear urban signal of phenotypic change and reveal variable effects of urban disturbance mechanisms. Observed effects might be due to the multiple challenges that urbanization poses on adaptation. Multiple influences can increase the total strength of selection on a trait, or the number of traits under selection (20).

**Urban Disturbance Mechanisms.** Urban Disturbance represents coupled mechanisms through which urban development affects natural processes and evolutionary dynamics. Model predictions highlight two categories driving the urban signature: social interactions and biotic interactions, specifically introduction of predators, prey, hosts, and competitors. Anthropogenic habitat modification had a lower than expected impact. The assessment of the effect of

the various urban disturbances should be interpreted cautiously since it might reflect the classification of interrelated disturbances, and the nature of species observed in available studies.

**Habitat modification.** Land cover conversion and loss of native habitat are major drivers of contemporary evolution. The observed counterintuitive lower phenotypic change associated with Habitat Modification relative to the Natural context in our study may reflect in part the vagility of birds generally, and an overrepresentation in the database of studies finding stable migration phenology of European birds in particular. It also might be due to the fact that habitat modification is captured by other interrelated urban disturbance classes and by other variables such as  $\Delta$  City Lights that show the expected trend of greater phenotypic change. Urban-driven habitat modification can affect species traits and composition. For example, changes in climate, artificial lighting, and availability of food are all 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–rural gradient (22).

**Biotic interactions.** We determined that introduction of predator, prey, host, or competition contributes to a higher rate of phenotypic change compared with 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. This might result in colonization, as more frequent introductions of exotic species translate into invasions (23). For example, McDonnell and Hahs (24) found higher levels of earthworm biomass and abundance in urban forests compared with rural ones, likely because of introduced species. Urbanization also alters the way species distribute and interact (25). Marzluff (25) found that, although diversity still emerges as the balance between extinction and colonization, species invasion plays a prominent role.

**Heterogeneity.** At the community level, cities directly and indirectly affect phenotypic change 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 native species, but loss of functional heterogeneity driven by

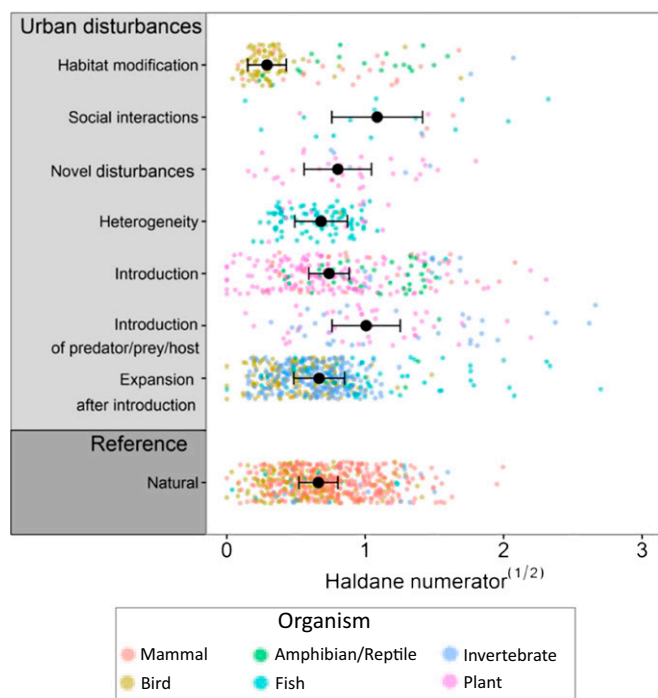
**Table 1.** Model-averaged coefficients from the full model set revealed several strong and many weak effects

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

Significance levels: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ ,  $^{\dagger}P < 0.1$ .

<sup>†</sup>Abbreviations: U. Dist., Urban Disturbance; HabMod, habitat modification; Hetero, heterogeneity; and subcategories of biotic interaction: Int, introduction; IntEco, introduction of predator/prey/host/competition; Expalnt, range expansion after introduction.





**Fig. 3.** Multimodel predictions for Urban Disturbance categories. Some categories were associated with relatively high phenotypic change (i.e., Social Interactions and Introduction of predator/prey/host/competitors), whereas others associated with background or even stable phenotypes (Habitat modification). Modeled, but not shown, variables were held constant at means (continuous variables) or reference values (categorical variables).

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). Phenotypic trait change within species, however, was not associated to heterogeneity in our analysis. Perhaps this is not surprising given that novel adaptations were allotted to a different process, and emphasis was placed on small-scale spatial heterogeneity where dispersion and gene flow is more likely.

**Novel disturbance.** 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. (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, ecotoxins 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). Low statistical power might have hindered a stronger observed effect.

**Social interactions.** Perhaps the most significant quality that distinguishes cities is their pace of change. Urbanization changes the dynamics of socioecological 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).

Socioeconomic shifts associated with urbanization can explain the emergence of a detectable urban signature of evolutionary change. 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. nonurban 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 ecoevolutionary implications of urban-driven phenotypic trait changes and identify existing gaps in knowledge. The evolution of antibiotic resistance, pesticide resistance, host–pathogen coevolution, and evolution in response to harvest and habitat change provide examples of the link between human-driven evolution and sustainability (37). Urban environments provide the context for many such interactions, bringing people into contact with novel pathogens, accelerating the spread of genes that confer resistance, and generally selecting for traits that enhance the survival and reproduction of 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 (38). However, adaptation can also enable the survival and reproduction of species that reduce biodiversity and human well-being. For example, evolution of pesticide resistance in agriculture and antibiotic resistance in human medicine represent critical threats to food security and human health (39, 40). Thus, evolution should take on a prominent role in the future of sustainability science.

Table 2 identifies examples of traits for which there is evidence of phenotypic changes in response to environmental changes driven by urbanization. The evolution of traits that control ecosystem processes could lead to significant changes in ecosystem functions (49). 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 (50). 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.

## Conclusions

Rapid urbanization poses new challenges for species—some will go extinct (at least locally), whereas others will adapt or relocate (51). Our paper asked whether we can detect distinct signatures of urban-driven phenotypic change across taxa and determine the extent to which systemic changes to socioecological systems associated with urban agglomerations might accelerate ecoevolutionary change. We found a clear urban signal of phenotypic change, and greater phenotypic change in urbanizing systems compared with natural and nonurban anthropogenic systems. By explicitly linking urban development to heritable traits that affect ecosystem function, we can begin to map the ecoevolutionary 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 insights for maintaining ecosystem function in the long term and can direct policy makers toward sustainability solutions (37).

## Materials and Methods

**Database on Rates of Phenotypic Change.** 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, ecoevolutionary, anthropogenic change, urban disturbances, and system stability). Studies were screened (*SI Appendix, Database Filtering*), and, if selected, phenotypic rates were extracted (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 synchronic for cross-sectional studies comparing samples obtained synchronously from populations derived from a common ancestral population. Rates were classified according to whether 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 dataset 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 population(s) of a species within a geographical region putatively exposed to similar environmental effects and high gene flow potential. We evaluated whether study systems were evolving in an anthropogenic vs. natural context (15), and the effect of Urban Disturbance (see next section).

**Urban Disturbance Classification and Georeferencing.** We use the global urban area map at 1-km spatial resolution developed by Zhou et al. (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 (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, habitat modification, heterogeneity, or novel disturbance (6) (*SI Appendix, Urban Disturbance Classification*). 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 in a new range following introduction vs. introduced species after range expansion. Heterogeneity can refer to heterogeneity in space or time. Novel disturbances require novel adaptations, for example, rapid evolution of zinc tolerance (42). Social interactions refer to direct or intentional results of human agency. Examples are listed in Table 2.

**Statistical Analyses.** We used an information-theoretic approach to rank statistical models and conduct multimodel inference, based on AICc (23, 55). 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 sample sizes (1,663 rates nested in 175 study systems). The statistical models were GLMMs. The response variable, phenotypic change (square-root transformed), was measured as the absolute magnitude of phenotypic change standardized by character variation (Haldane numerator; ref. 19, as formulated in ref. 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 modeled as a random effect, with combinations of background and urban variables (fixed effects):

$$\begin{aligned} H_{(i)}^{(1/2)} &= \alpha_{(j)} + \beta X_i + \varepsilon_i, \\ \alpha_j &\sim N(\mu, \sigma^2 \alpha), \\ \varepsilon &\sim N(0, \gamma), \end{aligned}$$

where the indexes  $i$  run from 1 to number of observations, and  $j$  run from 1 to number of study systems,  $H^{(1/2)}$  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,  $\beta$  is a vector of partial regression coefficients related to a matrix of explanatory variables  $X$ , and  $\varepsilon$  is the residual error with variance  $\gamma$ , which was modeled as follows:

$$\gamma = 0.1494 * (C + |\text{fitted}|^P)^2,$$

where  $C$  is a constant by stratum (0.3233 for genetic; 0.1249 for phenotypic), and  $P$  is an exponent of absolute fitted values by stratum (2.0754 for genetic;

**Table 2. Mapping urban-driven phenotypic trait change to ecosystem function**

Urban signatures			Ecoevolutionary feedback		Ref.
Urban Disturbance	Mechanism	Phenotypic trait	Ecosystem function	Feedback mechanism	
Novel	Exposure to effluent/heat from power plant	Physiological Heat coma temp. (thermal tolerance) in snails ( <i>Physa virgata</i> )	Biodiversity	New "physiological races"; colonization	41
Novel	Electricity pylons, novel high-zinc habitats	Zinc tolerance in plants: <i>Agrostis capillaris</i> , <i>Agrostis stolonifera</i> , etc.	Primary productivity; biodiversity	Consumer–resource dynamics	42
Heterogeneity	Hydrological connectivity altered via a fish ladder	Morphological Body size in brown trout ( <i>Salmo trutta</i> )	Nutrient cycling	Life history changes	43
Biotic interaction	Invasion of a molluskivorous crab ( <i>Carcinus maenas</i> )	Shell thickness (in millimeters) in periwinkle snail ( <i>Littorina obtusta</i> )	Biotic control	Trophic interactions	44
Social interaction	Long-term selective harvesting of a medicinal plant	Size of American ginseng plants ( <i>Panax quinquefolius</i> )	Primary productivity; biodiversity	Consumer–resource dynamics	45
Biotic interaction	Introduction to predator-free island	Behavioral Antipredator behavior in multiple species of marsupials	Nutrient cycling	Allocation of time to foraging vs. vigilance	46
Heterogeneity	Temporal heterogeneity in water availability	Phenological/life history Flowering time in field mustard ( <i>Brassica rapa</i> )	Primary production	Consumer–resource dynamics	47
Habitat modification	Global climate change	Seasonal onset of reproduction in 65 species of migratory birds	Biodiversity; biotic control	Colonization; novel competition	48

Documented phenotypic trait changes (see ref.), urban drivers, and hypothesized ecoevolutionary feedback mechanisms.

1.2376 for phenotypic). Hence, the chosen residual variance increased exponentially with fitted values, and slightly more so in genetic than phenotypic rates (*SI Appendix, Materials and Methods—Statistical Analysis*).

We used exploratory multimodel inference to assess the relative importance of predictor variables for phenotypic change, and to make predictions about contrasting urban-related scenarios that considered information contained in all models. From three background plus six urban variables, we combined nine predictor variables to form  $2^9 = 512$  models, including a null model (intercept only), and excluding interactions. All models were fitted through maximum likelihood in the R package nlme (56). Models were ranked according to decreasing values of AICc (57), and further evaluated using standard methods after refitting through restricted maximum-likelihood estimation (58). 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 MuMin, version 1.15.6 (55) (*SI Appendix, Materials and Methods—Statistical Analysis*).

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- Post DM, Palkovacs EP (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: Interactions between the ecological theatre and the evolutionary play. *Philos Trans R Soc Lond B Biol Sci* 364(1523):1629–1640.
- Pimentel D (1961) Animal population regulation by the genetic feed-back mechanism. *Am Nat* 95(881):65–79.
- Schoener TW (2011) The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. *Science* 331(6016):426–429.
- Matthews B, et al. (2011) Toward an integration of evolutionary biology and ecosystem science. *Ecol Lett* 14(7):690–701.
- Palkovacs EP, Kinnison MT, Correa C, Dalton CM, Hendry AP (2012) Fates beyond traits: Ecological consequences of human-induced trait change. *Evol Appl* 5(2):183–191.
- Alberti M (2015) Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol Evol* 30(2):114–126.
- United Nations, Department of Economic and Social Affairs, Population Division (2014) *World Urbanization Prospects: The 2014 Revision: Highlights (ST/ESA/SER/A/352)* (Department of Economic and Social Affairs, Population Division, United Nations, New York).
- Seto KC, Güneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc Natl Acad Sci USA* 109(40):16083–16088.
- Liu J, et al. (2013) Framing sustainability in a telecoupled world. *Ecol Soc* 18(2):26.
- Marzluff JM, Angell T (2005) Cultural coevolution: How the human bond with crows and ravens extends theory and raises new questions. *J Ecol Anthropol* 9(1):69–75.
- Hasselman DJ, et al. (2014) Human disturbance causes the formation of a hybrid swarm between two naturally sympatric fish species. *Mol Ecol* 23(5):1137–1152.
- Partecke J (2013) Mechanisms of phenotypic responses following colonization of urban areas: From plastic to genetic adaptation. *Avian Urban Ecology: Behavioural and Physiological Adaptations*, eds Gil D, Brumm H (Oxford Univ Press, Oxford, UK), p 131.
- Hendry AP, Kinnison MT (1999) Perspective: The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* 53(6):1637–1653.
- Kinnison MT, Hendry AP (2001) The pace of modern life II: From rates of contemporary microevolution to pattern and process. *Genetica* 112–113:145–164.
- Hendry AP, Farrugia TJ, Kinnison MT (2008) Human influences on rates of phenotypic change in wild animal populations. *Mol Ecol* 17(1):20–29.
- Crispo E, et al. (2010) The evolution of phenotypic plasticity in response to anthropogenic disturbance. *Evol Ecol Res* 12(1):47–66.
- Gotanda KM, Correa C, Turcotte MM, Rolshausen G, Hendry AP (2015) Linking macro-trends and micro-rates: Re-evaluating microevolutionary support for Cope's rule. *Evolution* 69(5):1345–1354.
- Anderson DR (2008) *Model Based Inference in the Life Sciences: A Primer on Evidence* (Springer, New York), 1st Ed.
- Haldane JB (1949) Suggestions as to quantitative measurement of rates of evolution. *Evolution* 3(1):51–56.
- Nosil P, Harmon LJ, Seehausen O (2009) Ecological explanations for (incomplete) speciation. *Trends Ecol Evol* 24(3):145–156.
- Winkel W, Hudde H (1997) Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and pied flycatchers *Ficedula hypoleuca*. *J Avian Biol* 28(2):187–190.
- Mittelbach GG, et al. (2001) What is the observed relationship between species richness and productivity? *Ecology* 82(9):2381–2396.
- Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. *Bioscience* 55(5):399–407.
- McDonnell M, Hahs A (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: Current status and future directions. *Landsc Ecol* 23(10):1143–1155.
- Marzluff JM (2005) Island biogeography for an urbanizing world: How extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosyst* 8(2):157–177.
- Pickett STA, et al. (2017) Dynamic heterogeneity: A framework to promote ecological integration and hypothesis generation in urban systems. *Urban Ecosyst* 20:1–14.
- Aronson MFJ, et al. (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc R Soc B* 281(1780):20133330.
- Groffman PM, et al. (2014) Ecological homogenization of urban USA. *Front Ecol Environ* 12(1):74–81.
- Rebele F (1994) Urban ecology and special features of urban ecosystems. *Glob Ecol Biogeogr* 4(6):173–187.
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol Evol* 21(4):186–191.
- Pickett STA, Wu J, Cadenasso ML (1999) Patch dynamics and the ecology of disturbed ground: A framework for synthesis. *Ecosystems of Disturbed Ground*, ed Walker LR (Elsevier Science, Amsterdam).
- Cardinale BJ, Hillebrand H, Charles DF (2006) Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. *J Ecol* 94(3):609–618.
- Kille P, et al. (2013) DNA sequence variation and methylation in an arsenic tolerant earthworm population. *Soil Biol Biochem* 57:524–532.
- Shenoy K, Crowley PH (2011) Endocrine disruption of male mating signals: Ecological and evolutionary implications. *Funct Ecol* 25(3):433–448.
- Bettencourt LMA (2013) The origins of scaling in cities. *Science* 340(6139):1438–1441.
- Clucas B, Marzluff JM (2012) Attitudes and actions toward birds in urban areas: Human cultural differences influence bird behavior. *Auk* 129(1):8–16.
- Carroll SP, et al. (2014) Applying evolutionary biology to address global challenges. *Science* 346(6207):1245993.
- Chislock MF, Sarnelle O, Jernigan LM, Wilson AE (2013) Do high concentrations of microcystin prevent *Daphnia* control of phytoplankton? *Water Res* 47(6):1961–1970.
- Gluckman PD, Low FM, Buklijas T, Hanson MA, Beedle AS (2011) How evolutionary principles improve the understanding of human health and disease. *Evol Appl* 4(2):249–263.
- Thrall PH, et al. (2011) Evolution in agriculture: The application of evolutionary approaches to the management of biotic interactions in agro-ecosystems. *Evol Appl* 4(2):200–215.
- McMahon RF (1976) Effluent-induced interpopulation variation in the thermal tolerance of *Physa virgata* Gould. *Comp Biochem Physiol A* 55(1):23–28.
- Al-Hiyali SAK, McNeilly T, Bradshaw AD (1990) The effect of zinc contamination from electricity pylons. Contrasting patterns of evolution in five grass species. *New Phytol* 114(2):183–190.
- Haugen TO, Aass P, Stenseth NC, Vøllestad LA (2008) Changes in selection and evolutionary responses in migratory brown trout following the construction of a fish ladder. *Evol Appl* 1(2):319–335.
- Trussell GC, Smith LD (2000) Induced defenses in response to an invading crab predator: An explanation of historical and geographic phenotypic change. *Proc Natl Acad Sci USA* 97(5):2123–2127.
- McGraw JB (2001) Evidence for decline in stature of American ginseng plants from herbarium specimens. *Biol Conserv* 98(1):25–32.
- Blumstein DT, Daniel JC (2003) Foraging behavior of three Tasmanian macropodid marsupials in response to present and historical predation threat. *Ecography* 26(5):585–594.
- Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc Natl Acad Sci USA* 104(4):1278–1282.
- Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proc Biol Sci* 270(1523):1467–1471.
- Odling-Smee FJ, Laland KN, Feldman MW (2003) *Niche Construction: The Neglected Process in Evolution* (Princeton Univ Press, Princeton).
- Bouma TJ, De Vries MB, Herman PMJ (2010) Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. *Ecology* 91(9):2696–2704.
- Marzluff JM (2012) Urban evolutionary ecology. *Stud Avian Biol* 45:287–308.
- Zhou Y, et al. (2015) A global map of urban extent from nightlights. *Environ Res Lett* 10(5):54011.
- Zhou Y, et al. (2014) A cluster-based method to map urban area from DMSP/OLS nightlights. *Remote Sens Environ* 147:173–185.
- Ellis EC, Ramankutty N (2008) Putting people in the map: Anthropogenic biomes of the world. *Front Ecol Environ* 6(8):439–447.
- Barton K (2016) Package “MuMIn”: Multi-Model Inference. R package, Version 1.15.6. Available at <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>. Accessed August 9, 2016.
- Pinheiro J, Bates D, DebRoy S, Heisterkamp S, Van Willigen B (2016) Package “nlme.” Available at <https://cran.r-project.org/web/packages/nlme/nlme.pdf>. Accessed August 5, 2016.
- Burnham KP, Anderson DR (2003) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, New York), 2nd Ed.
- Zuur AF, et al. (2009) *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York).