

Global urban signatures of phenotypic change in animal and plant populations

Marina Alberti^{a,1}, Cristian Correa^b, John M. Marzluff^c, Andrew P. Hendry^{d,e}, Eric P. Palkovacs^f, Kiyoko M. Gotanda^g, Victoria M. Hunt^a, Travis M. Appgar^f, and Yuyu Zhou^h

^aDepartment of Urban Design and Planning, University of Washington, Seattle, WA 98195; ^bInstituto de Conservación, Biodiversidad y Territorio, Universidad Austral de Chile, Casilla 567, Valdivia, Chile; ^cSchool of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195; ^dRedpath Museum, McGill University, Montreal, QC, Canada H3A0C4; ^eDepartment of Biology, McGill University, Montreal, QC, Canada H3A0C4; ^fDepartment of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060; ^gDepartment of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom; and ^hDepartment of Geological and Atmospheric Sciences, Iowa State University, Ames, IA 50011

Edited by Jay S. Golden, Duke University, Durham, NC, and accepted by Editorial Board Member B. L. Turner October 31, 2016 (received for review August 2, 2016)

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

Emerging 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 km², 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.

Author contributions: M.A., C.C., J.M.M., A.P.H., E.P.P., K.M.G., and V.M.H. designed research; M.A., A.P.H., E.P.P., K.M.G., V.M.H., T.M.A., and Y.Z. performed research; C.C. analyzed data; and M.A., C.C., J.M.M., A.P.H., E.P.P., K.M.G., and V.M.H. wrote the paper. The authors declare no conflict of interest.

This article is a PNAS Direct Submission. J.S.G. is a Guest Editor invited by the Editorial Board.

¹To whom correspondence should be addressed. Email: malberti@uw.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1606034114/-DCSupplemental.

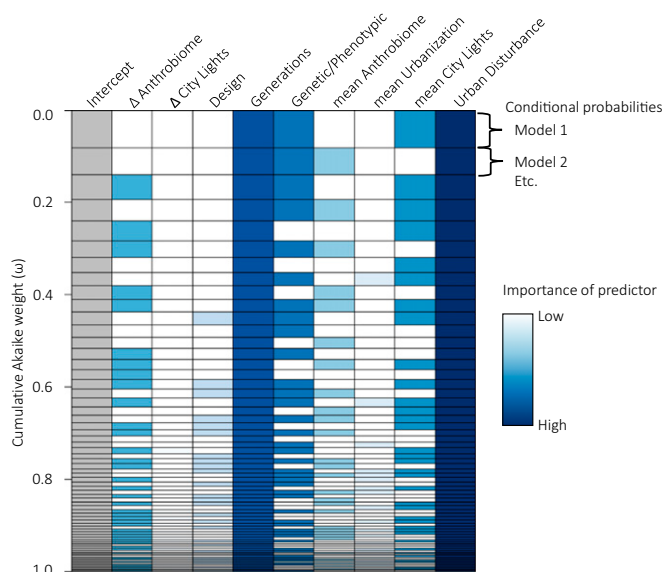


Fig. 2. Representation of the AICc model selection table. Rows represent models sorted by decreasing empirical support (row height represents model probability conditional on the full model set). Predictor variables were shaded if included in a model. Saturation corresponded to estimated variable relative 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., Δ 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 Δ 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 [†]	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
Δ City Lights	0.072	0.031	2.344	0.019*
Mean Anthrobiome	−0.009	0.008	1.141	0.254
Δ 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: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, $^{\dagger}P < 0.1$.

[†]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.

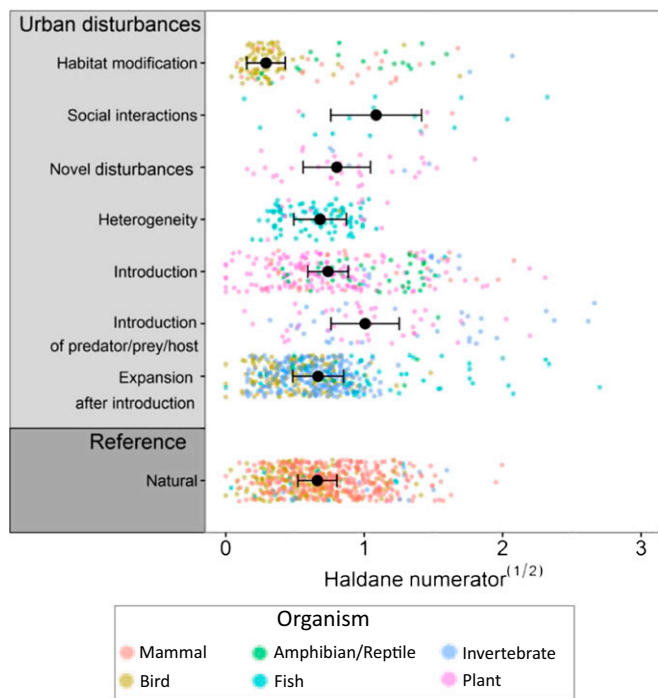


Fig. 3. Multimodel predictions for Urban Disturbance categories. Some categories were associated with relatively high phenotypic change (i.e., Social Interactions and Introduction of predator/prey/host/competitors), whereas others associated with background or even stable phenotypes (Habitat modification). 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):

$$H_{(i)}^{(1/2)} = \alpha_{j(i)} + \beta X_i + \varepsilon_i,$$

$$\alpha_j \sim N(\mu, \sigma^2 \alpha),$$

$$\varepsilon \sim N(0, f(\gamma)),$$

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), α is normally distributed with mean μ (overall intercept) and variance $\sigma^2 \alpha$, allowing for varying intercepts per study system, β is a vector of partial regression coefficients related to a matrix of explanatory variables X , and ε is the residual error with variance γ , 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*).

ACKNOWLEDGMENTS. We thank the John D. and Catherine T. MacArthur Foundation for partially supporting the study (Grant 14-106477-000-USP). C.C. was funded by Comisión Nacional de Investigación Científica y Tecnológica-Programa de Atracción e Inserción de Capital Humano Avanzado (CONICYT-PAI) Grant 82130009 and Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT) Grant 11150990.

- 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.
- Hasselmann 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. *Landscape 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. (2016) Dynamic heterogeneity: A framework to promote ecological integration and hypothesis generation in urban systems. *Urban Ecosyst*, in press.
- 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-Hiyaly 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, ed (2009) *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York).

Supporting Information

Global urban signatures of phenotypic change in animal and plant populations

Marina Alberti et al.

Contents

1. Database filtering	1
2. Urban Disturbance Classification.....	4
3. Gauging the urban signature beyond the anthropogenic context	5
4. Materials and Methods – Statistical analysis.....	10

1. Database filtering

We analyzed a modified and geo-referenced version of a database of rates of phenotypic change (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 S1). Since the objective of this study was to conduct exploratory statistical analyses to gauge the potential effects of urbanization on an organism's phenotypic change, we focused on a small subset of the original database for which minimum necessary information was available. We further reduced the data set in an attempt to achieve fair comparisons (i.e., unbiased model coefficient estimates). Thus, the database was subjected to a series of filters before conducting the statistical analyses (Table S1).

We began with version V4.04 of the database, which included >11 thousand rates nested in 379 study systems, and 309 species reported in 146 studies. First, the number of rates was reduced by about half by excluding pairwise allochronic contrasts while retaining the first and last samples of each time series. We did not want the analyses to be dominated by a few, long time series. Then we retained rates measured in the range of [1, 300] generations, which allowed the retention of most rates while focusing exclusively on microevolutionary time. We measured phenotypic change in Haldane numerators (see 4: *Materials and Methods*), and discarded rows unable to produce that response variable. Haldanes make use of samples' pooled standard deviations, and cases with extremely heteroscedasticity (F-ratio between samples >25) or very small standard deviations ($SD < 0.001$) were excluded. These cases are commonly produced by insufficient sampling or other sources of error. Many of our analyses involved spatial analyses, and samples lacking geographic coordinates were excluded. A number of samples did have geographic coordinates but nonetheless failed to produce Anthropogenic Biome (Anthrobiome) data. These were also excluded. Finally, we were concerned that Synchronic rates involving samples measured across very different ecological contexts would add substantial noise to our analyses. We retained only rates calculated from samples sharing an ecoregion. Ecoregion, in this case, corresponded to terrestrial ecoregion

(preferred) or marine ecoregion from The Nature Conservancy's terrestrial and marine ecoregion GIS data layers (available at http://maps.tnc.org/gis_data.html) (Table S2).

Table S1: Filters applied to the dataset before conducting statistical analyses. Numbers refer to the sample size for the given variable after filtering.

Sequential filtering	Rates	Systems	Species	References
Database_V4.04 (original data source)	11360	379	309	146
Pairwise allochronic comparisons excluded	5318	375	305	142
Generations <1 excluded	5313	375	305	142
Generations >300 excluded	5228	366	302	141
Incomplete for Haldanes excluded	4388	257	201	130
F-ratio between samples >25 excluded	4284	249	193	130
Samples with SD < 0.001 excluded	4274	249	193	129
Non-georeferenced samples excluded	2894	191	169	112
Samples missing Anthrobiome data excluded	2805	185	163	106
Samples from different Ecoregions excluded	1663	175	155	89

Table S2: List of ecoregions detected for locations included in the database. Each location (lat-lon) received one of The Nature Conservancy's terrestrial (preferred) or marine ecoregions (<http://maps.tnc.org/files/metadata/TerrEcos.xml>). Only rates obtained from samples sharing ecoregion were included in the analyses.

Ecoregion
Boreal Forests/Taiga
Deserts and Xeric Shrublands
Flooded Grasslands and Savannas
Inland Water
Mangroves
Mediterranean Forests, Woodlands and Scrub

Montane Grasslands and Shrublands
 Temperate Broadleaf and Mixed Forests
 Temperate Conifer Forests
 Temperate Grasslands, Savannas, and Shrublands
 Temperate Northern Atlantic
 Temperate Northern Pacific
 Tropical and Subtropical Coniferous Forests
 Tropical and Subtropical Grasslands, Savannas, and Shrublands
 Tropical and Subtropical Moist Broadleaf Forests
 Tundra

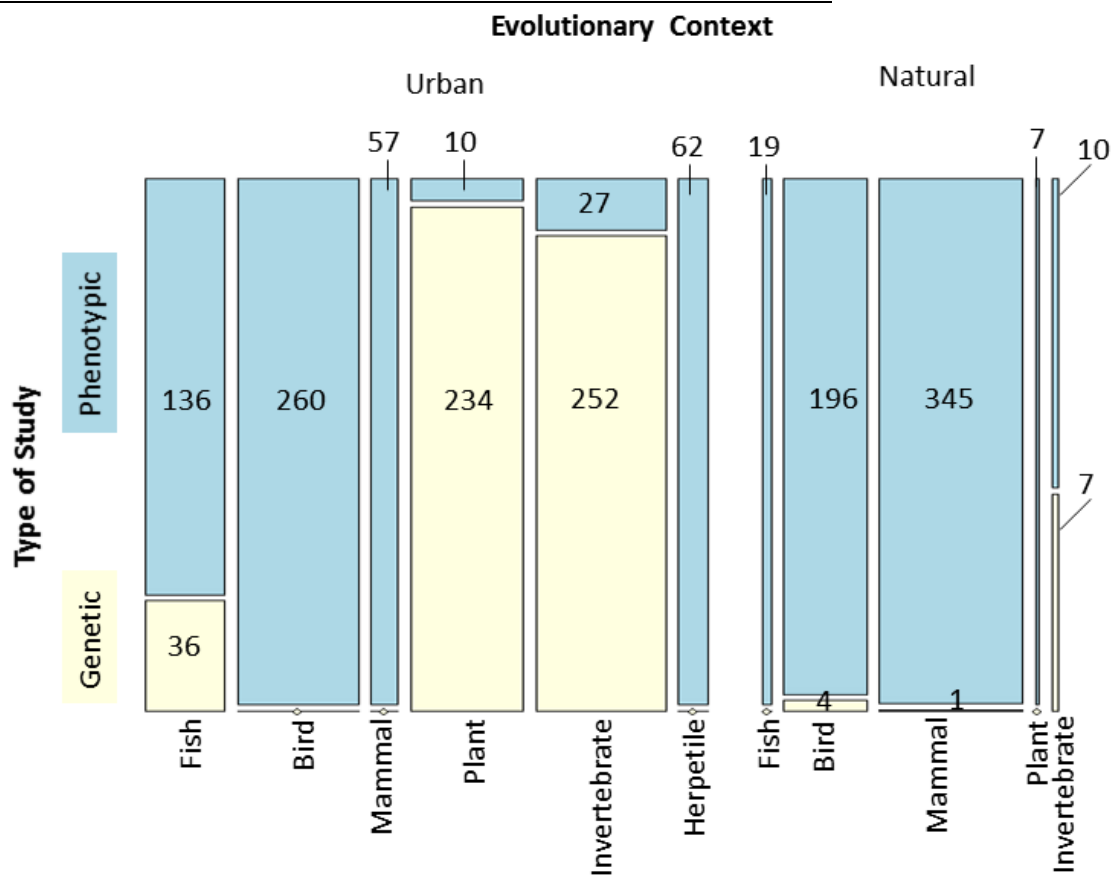


Figure S1 Summary of geo-referenced database of phenotypic change experimental and observational studies included in this study. Numbers in the mosaic plot tiles refer to the number of phenotypic rates in specific categories.

2. Urban Disturbance Classification

We classified *Urban Disturbances* for all systems in which the driver of evolutionary change is anthropogenic. For samples in applicable study systems, we then classified the *Urban Disturbance* as social interaction, biotic interaction (with subcategories for native species responding to introductions vs. introduced species immediately following introduction or expanding its range following an introduction), habitat modification, heterogeneity, or novel disturbance (6). To classify *Urban Disturbances*, we developed a classification tree (Fig. S2). We defined habitat modification to represent changes due to climate change in general, modification of the landscape, or pollution. Biotic interactions stem from introductions, and are subcategorized depending on the study organism's ecological role: introduced species, or species in its native range responding to an introduction. Introduced species were further subdivided into instances where the introduced species adapts immediately following introduction, vs. adaptation after range expansion (post introduction). Heterogeneity may refer to micro-habitat or micro-climate, and can refer to heterogeneity in space or time. Novel disturbances were defined as those disturbances to which organisms respond to with novel adaptations, such as the rapid evolution of zinc tolerance (42). Social interactions refer to disturbances with are the direct and intentional result of human agency.

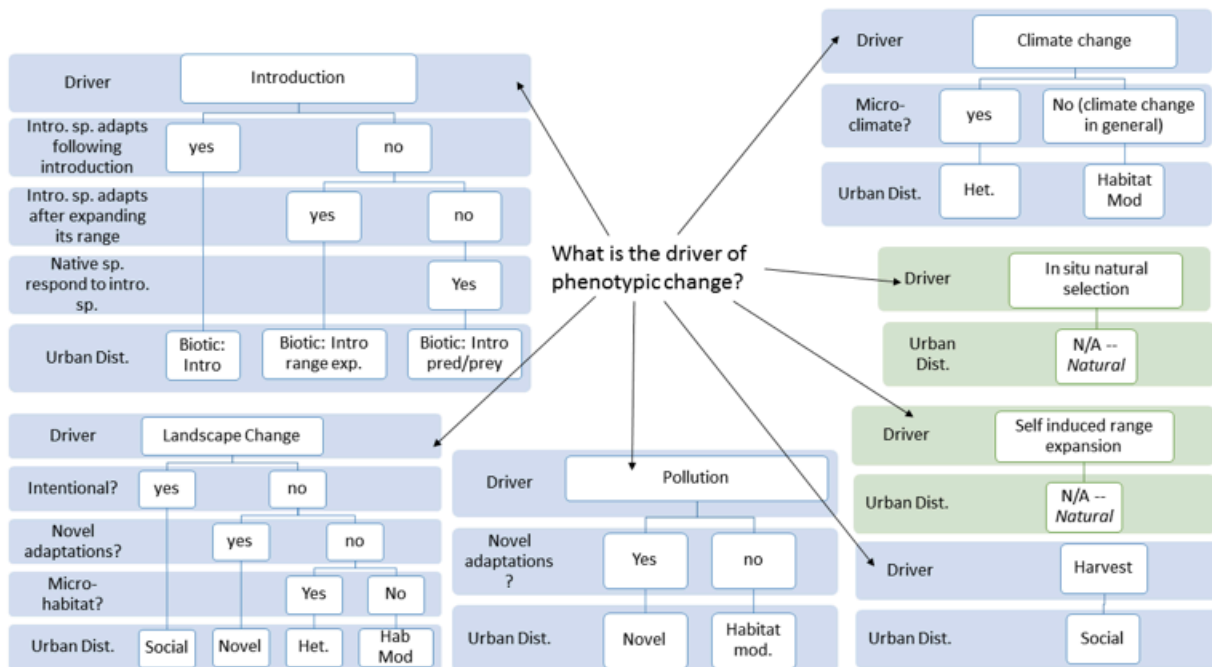


Figure S2 Classification tree for systematic determination of *Urban Disturbances*.

3. Gauging the urban signature beyond the anthropogenic context

In this section we asked if urban variables (main article) could explain phenotypic change while accounting for the previously described effect of anthropogenic context and other putatively important variables (15, see below). Since anthropogenic context (15) is obviously related to urban variables, it was unclear whether urban variables would add explanatory power. To gauge the importance of potential urban effects on phenotypic change while accounting for additional known effects, we conducted a preliminary analysis of potential urban effects on phenotypic change while accounting for additional known effects. The results showed that urban variables provide substantial additional information for explaining phenotypic change, thus warranting further analyses and interpretations of our study. In addition, this approach allowed us to measure the correlations between estimated model coefficients of background variables and putatively informative urban variables, which informed about how redundant variables were in explaining patterns in the data.

We began by creating a set of 19 statistical models divided into two groups: the first group (models #1-3) included important known effects on rates of phenotypic change, namely the effect of variables *Context*, *Generations*, *Design*, and *GenPhen* (see references in the main article). Henceforth we call these variables background variables, to distinguish them from urban variables (main article). The second group of models included both background variables and urban variables (models #4-19; Table S3). The rationale for including background variables *a priori* in all models was to ensure that any urban-related signal that might be detected would represent an addition to the current state of knowledge and not a mere topological substitution. This is particularly relevant since the previously known effect of context (anthropogenic associated to higher phenotypic change; 15) is potentially related with the effect of our urban-related variables—especially with *Urban Disturbance* which essentially is a finer classification of context.

All 19 models were generalized linear mixed-effect models (GLMM), designed to statistically explain phenotypic change measured as Haldane numerator^(1/2), and were fitted to our dataset through maximum likelihood (ML) in the R package nlme (56). All models had the same variance structure function (`varComb(varIdent(form= ~ 1|GenPhen), varPower(form= ~fitted(.)))`) that allowed for the residual error to increase with fitted values (power = 1.0514) after a slight intercept shift per GenPhen group (phenotypic = 1.0000; genotypic = 0.0854). (This variance structure was chosen amongst 19 alternatives (not shown), following the approach described in Supplementary Information, 4. *Materials and Methods – Statistical analysis*.) All models also had the same random effect of *Study system* in order to account for the nested structure of the data. Models were ranked according to decreasing values of second-order Akaike Information Criteria AICc (57), and further evaluated using standard methods after re-fitting through REML estimation (58).

We found a consistent supremacy of models that included urban variables while accounting for the effect of background variables. In fact, every one of the models with any relative support included at least one urban variable ($Wt > 0.00$ in Table S3). In particular, every top-ranked model

included Urban Disturbance, and three urbanization proxies (Mean Urbanization, Mean Anthrobiome and Delta Anthrobiome) also contributed. Despite the 95% confidence set including only five models, no model received a particularly high weight, indicating high model uncertainty.

As mentioned earlier, there was a logical association between *Context* (15) and our urban variables. Therefore, model coefficients were expected to be confounded to some extent due to predictor collinearity. It is therefore noteworthy that despite the inclusion of *Context* in every model, there was still substantial empirical support for at least some focal urban-related variables. Closer examination of the top-ranked model serves to illustrate these points. The AICc-best model (m11; Table S3) included the fixed effects of four background and two urban predictor variables (*Urban Disturbance* and *City Light*), in addition to the random effect of *Study system*, and a residual variance structure described above. The random effect of *Study system* was moderate with a correlation between two observations from the same study system, or intraclass correlation coefficient (ICC) of 0.116. Nevertheless this effect was highly significant suggesting that it is, at least partially, capturing the nested structure of our data set (LRT, Chi-squared = 632.7056, $P < 0.0001$). This model (m11) received approximately four-fold empirical support compared to that of m1, which was similar but devoid of urban variables (evidence ratio, $E_{m1, m11} = 4.21$). This translates in a highly significant improvement of model fit through the joint inclusion of urban variables *Urban Disturbance* and *Mean City Lights* (LRT, m1 vs. m11, Chi-squared = 91.951, $P < 0.0001$). Furthermore, the ANOVA table of the fixed effects of m11 reveals a very rich structure with all terms being significant or marginally so (Table S4). *Urban Disturbance* accounted for a significant fraction of the variation in phenotypic change, yet the predicted effect of *Urban Disturbance* appears confounded by *Context* (Fig. S3). This is also evident from the relatively high correlations between estimated partial regression coefficients of *Urban Disturbance* and *Context* (Fig. S4), which caused troublesome variance inflation factors (VIFs > 3, 58)

In conclusion, at least some of the urban variables contributed substantial novel information to explaining the patterns of contemporary phenotypic change found in nature. As expected, the effect of urban disturbance was confounded by the effect of anthropogenic context due to collinearity, but this did not preclude the former variable from receiving strong empirical support. In order to gain additional insights about the effect of urbanization, subsequent analyses (main article) were conducted omitting the correlated and confounding anthropogenic context variable.

Table S3. Model selection table (top seven models).

ID	Fixed terms	K	LL	AICc	Δ AICc	Wt	Cum. Wt
m11	ABCDGI	17	-417.40	869.16	0.00	0.24	0.24
m14	ABCDGL	17	-417.47	869.32	0.15	0.22	0.46
m4	ABCDG	16	-418.67	869.66	0.50	0.19	0.64
m13	ABCDGK	17	-417.76	869.90	0.73	0.16	0.81
m17	ABCDGKL	18	-416.90	870.23	1.06	0.14	0.95
m12	ABCDGJ	17	-419.16	872.70	3.53	0.04	0.99
m16	ABCDGHI	18	-419.90	876.22	7.06	0.01	0.99

Notes: Models were sorted by increasing values of second-order Akaike information criterion (AICc), and only the top-seven models (out of 19) were listed (i.e., those with Wt > 0.00). Fixed terms definitions: *Context* (A), *Design* (B), *Generations* (C), *GenPhen* (D), interaction *Generations:GenPhen* (E), interaction *Context:Generations* (F), *Urban Disturbance* (G), *Delta City Lights* (H), *Mean City Lights* (I), *Mean Urbanization* (J), *Delta Anthrobiome* (K), *Mean Anthrobiome* (L). Other variables are: K, number of parameter estimates; LL, log-likelihood; Wt, conditional model probability or Akaike weight (model likelihood of model *i* divided by the sum of model likelihoods); and Cum. Wt, cumulative Akaike weight.

Table S4. Anova table of the AICc-best model (m11).

Fixed term	Num DF	Den DF	F-value	p-value
GenPhen	1	1485	12.122	0.001
Context	1	167	64.870	0.000
Design	1	1485	10.332	0.001
Generations	1	1485	53.893	0.000
Urban Disturbance	7	167	16.261	0.000
Mean City Lights	1	1485	2.936	0.087

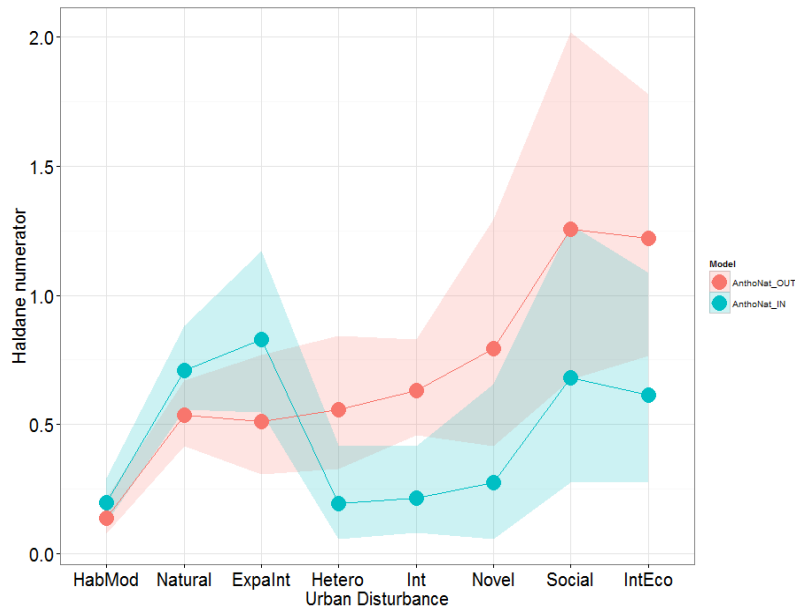


Fig. S3. Predictive effects of *Urban Disturbance*. Mean expected values (and 95% CI) of phenotypic change predicted from the best fitting model (blue), or a modified version of the model with *Context* removed (see model terms in Table S1). Note how model predictions are conditional on the inclusion of *Context*, owing to collinearity issues. Terms not plotted were set to constant means or reference values. *Urban Disturbance* categories in the x-axis were organized in ascending order of mean predictive discrepancies between models.

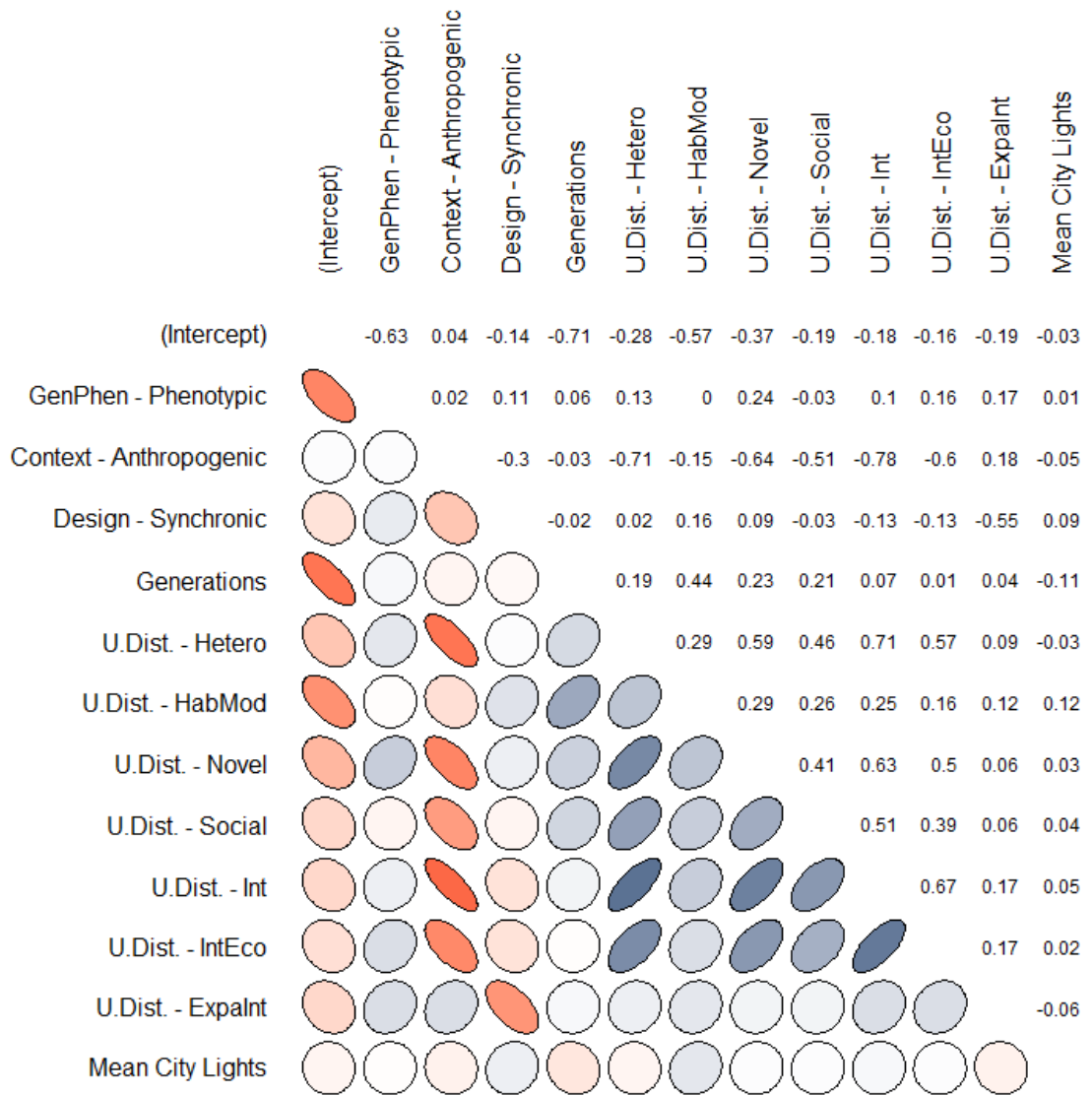


Fig. S4. Correlations between partial regression coefficients of the top model (m11). Positive and negative correlations were represented by cold and warm colors, respectively. Note how high correlations were observed between parameter estimates of *Context* and *Urban Disturbance* due to collinearity issue. Key for model parameter abbreviations: *Urban Disturbance* (U. Dist.), habitat modification (HabMod), heterogeneity (Hetero), introduction (Int), introduction of predator/prey/host/competition (IntEco), range expansion after introduction (Expalnt).

4. Materials and Methods – Statistical analysis

This section follows a full description of the statistical analyses outlined in the main article. We adopted an information-theoretic approach to conduct statistical model ranking and multimodel inference based on second order Akaike Information Criterion (AICc) (18, 57). 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) in which phenotypic change was set as the response variable (square-root transformed), and was measured as the absolute magnitude of phenotypic change standardized by character variation, a quantity known as the Haldane numerator (19 as formulated in 13).

Generalized mixed-effects models

Because the data had a hierarchical structure, study system was always modelled as a random effect, with combinations of background and urban variables modelled as fixed effects:

$$H^{(1/2)}_{(i)} = \alpha_{j(i)} + \beta X_i + \mathcal{E}_i$$

$$\alpha_j \sim N(\mu, \sigma^2\alpha)$$

$$\mathcal{E} \sim N(0, f(\gamma))$$

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), α is normally distributed with mean μ (overall intercept) and variance $\sigma^2\alpha$, allowing for varying intercepts per study system, β a vector of partial regression coefficients related to a matrix of explanatory variables X , and \mathcal{E} , the residual error with variance γ . The random effect of study system was moderate and always highly significant, capturing at least partially the structure of our hierarchical data set [the global model with nine predictor variables (see below) had ICC = 0.173, and was significantly different from a similar model without the random effect of study system (LRT, Chi-squared = 632.7056, $P < 0.0001$)].

Potential heteroscedasticity in residual variance (γ) in relation to fitted values and between groups of genetic vs. phenotypic rates (*GenPhen*) was evaluated by comparing 21 models differing only in their variance structure function (i.e., `varFunc` constructors in `nlme`; 56). A model with constant residual variance (homocedastic) was also included in the comparison. Model's fixed effects structure was held constant including all background and urban variables (nine variables in total). Model fitting was done through restricted maximum likelihood (REML) in the R environment (R version 3.2.5, R Core Team 2016) using the package `nlme` version 3.1-128 (56). The most suitable variance structure function was chosen by reference to the model with the lowest AICc

value, which was 2.05 lower than the second-best model. The selected model had the following residual variance structure:

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

where ν is a term of the estimated residual variance (0.1494), 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 modelled residual variance increased exponentially with fitted values, and slightly more so in genetic than phenotypic rates (Fig. S5). This heteroscedastic model significantly enhanced model fit compared to a homoscedastic model (LRT, Chi-squared = 302.3283, $P < 0.0001$). A visual inspection of standardized residuals plotted against fitted values showed little pattern (unlike the homoscedastic model), and the distribution of residuals was nearly normal (Figures S6-S7). All subsequent GLMMs used the selected variance structure function for modeling residual variance (58).

Multimodel inference

Multimodel inference offers a means to tap into information contained in a model set while weighing model uncertainty. It is especially suited for exploratory data analyses, like ours, that are constrained by lack of knowledge, small sample size, high dimensionality of predictor variables, and high variability (18). We used exploratory multimodel 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 at large.

From 3 background plus 6 urban variables, we combined 9 predictor variables to form $2^9 = 512$ models, including a null model (intercept only), and excluding interactions. The variable anthropogenic context (anthropogenic associated to higher phenotypic change; 15) was excluded because it was correlated with, and confounds the effect of, urban disturbance (Supporting Information: 3. *Gauging the urban signature beyond the anthropogenic context*). Some of the retained explanatory variables were correlated to a lesser extent producing variance inflation factors generally (93%) below 2.5 (max = 2.7), which is considered below the threshold to remove collinear variables (58). Consequently, all partial regression coefficients of the global model were below 0.62, which reinforced our decision to retain all 9 predictor variables in further analyses.

All models, which also contained the random effect of *Study system* and the residual variance structure function previously selected, were fitted through maximum likelihood (ML) in the R package nlme (56). Models were ranked according to decreasing values of AICc (57), and further evaluated using standard methods after re-fitting through REML estimation (58).

Predictor variable relative importance was calculated by the sum of the Akaike weights of all models containing a particular predictor variable. Urban disturbance variable was top-ranked, matched by $\log(\text{Generations})$ (Figure S8), which, once again supports the importance of this variable in our analyses. Model-averaged partial regression coefficients (see main article) were Akaike-

weighted averages of coefficients from all models containing a particular term (18). These coefficients allowed the illustration of effect sizes in terms of expected response (predictions) under particular scenarios (Table 1 and Figure 3, main article). For example, consistent with estimated variable relative importance, the range of predictions from different *Urban Disturbance* categories was higher than that of expected responses from varying background variables (Figure S9). Model ranking and inference was conducted in the R package MuMin v1.15.6 (55).

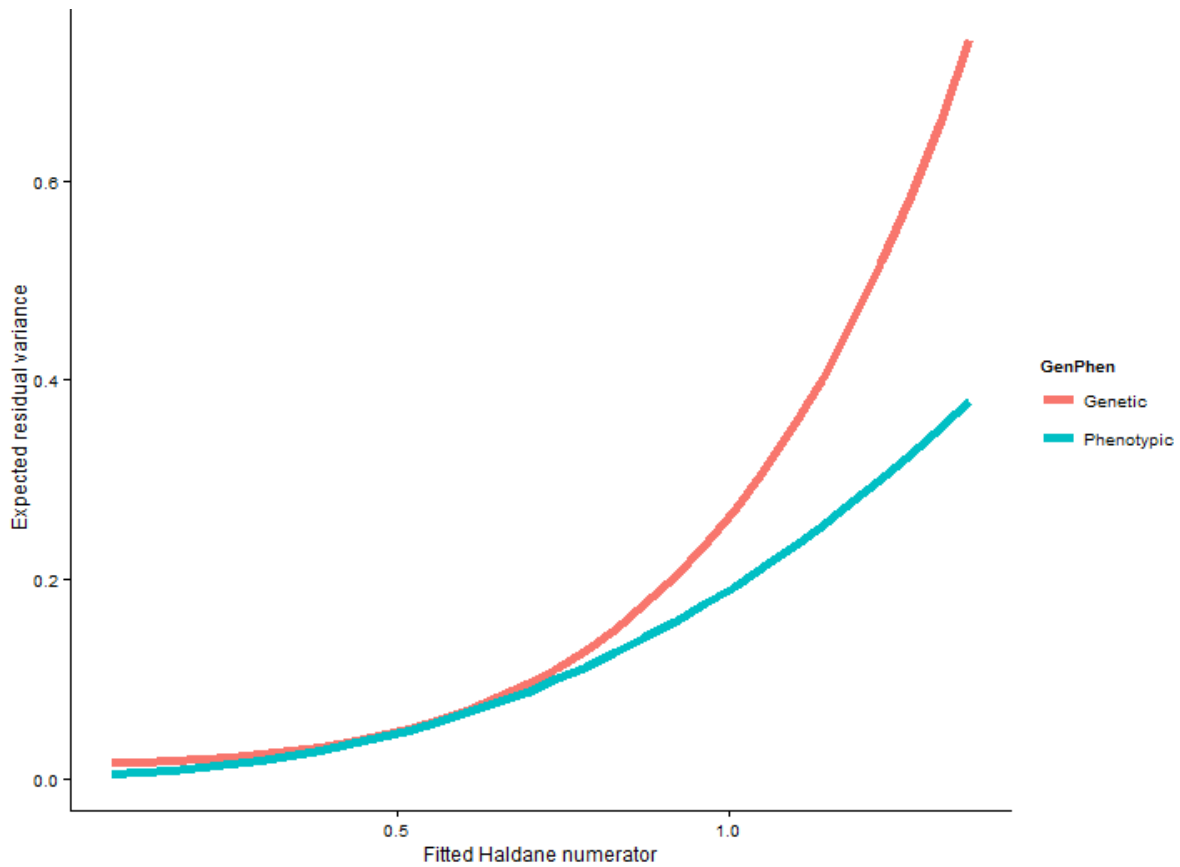


Figure S5: Selected model variance structure function. The expected residual variance increased exponentially with fitted values, and more so in genetic studies.

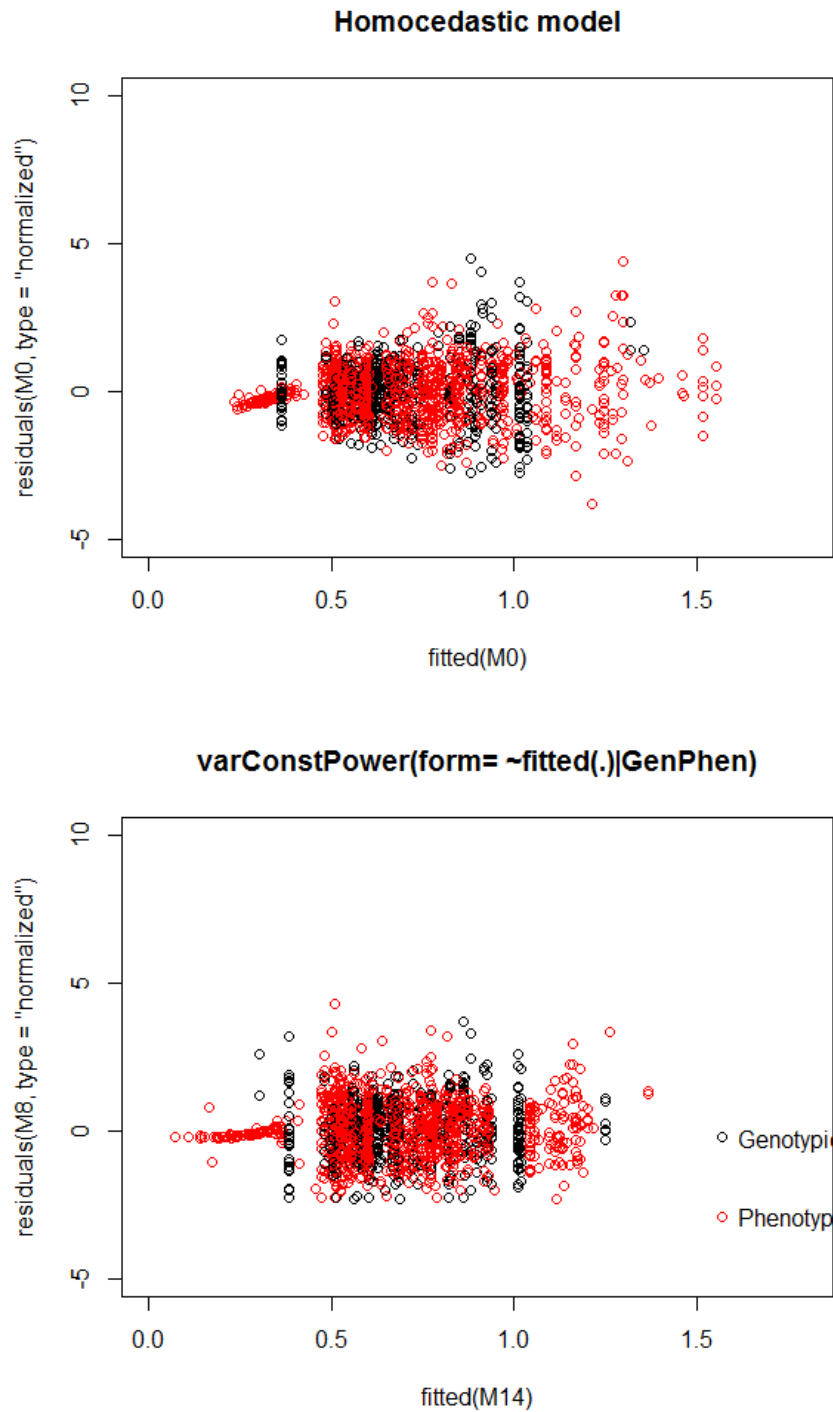


Figure S6: Standardized residual plots of (top) homoscedastic global model, and (bottom) of global model bearing the selected heteroscedastic residual variance structure function.

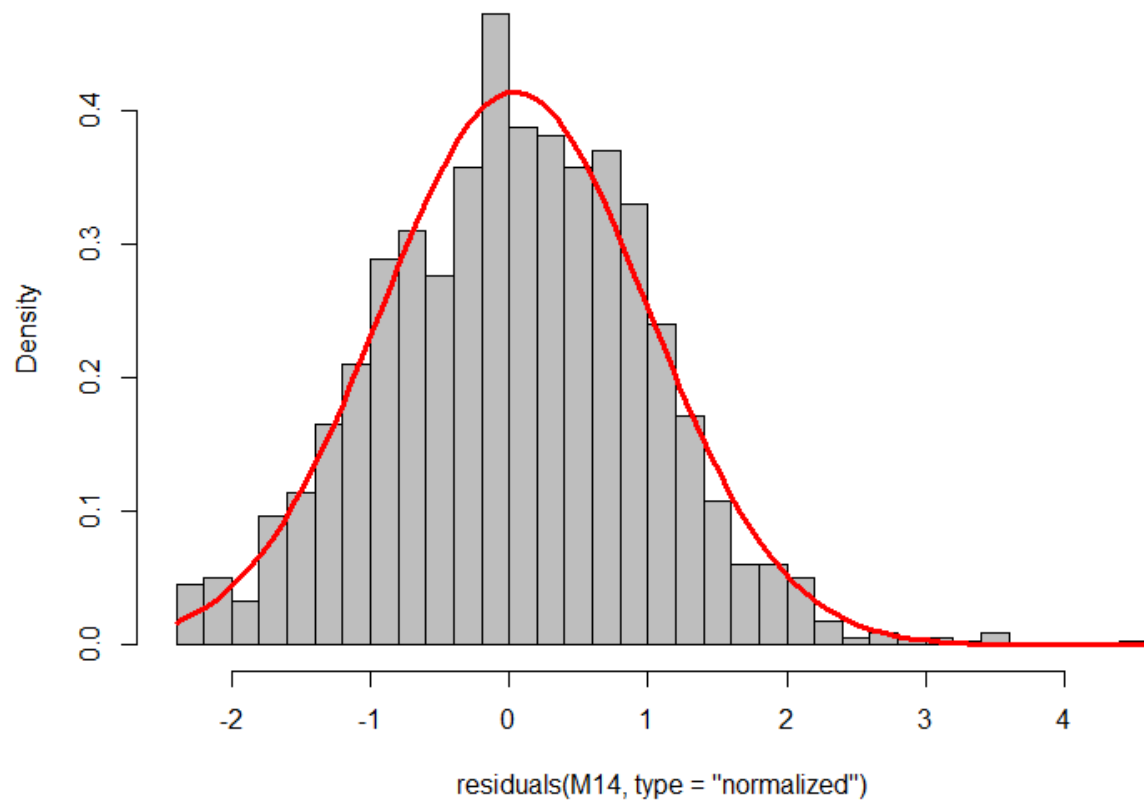


Figure S7: Frequency distribution of standardized residuals of global model (gray bars), and fitted normal probability density curve (red line).

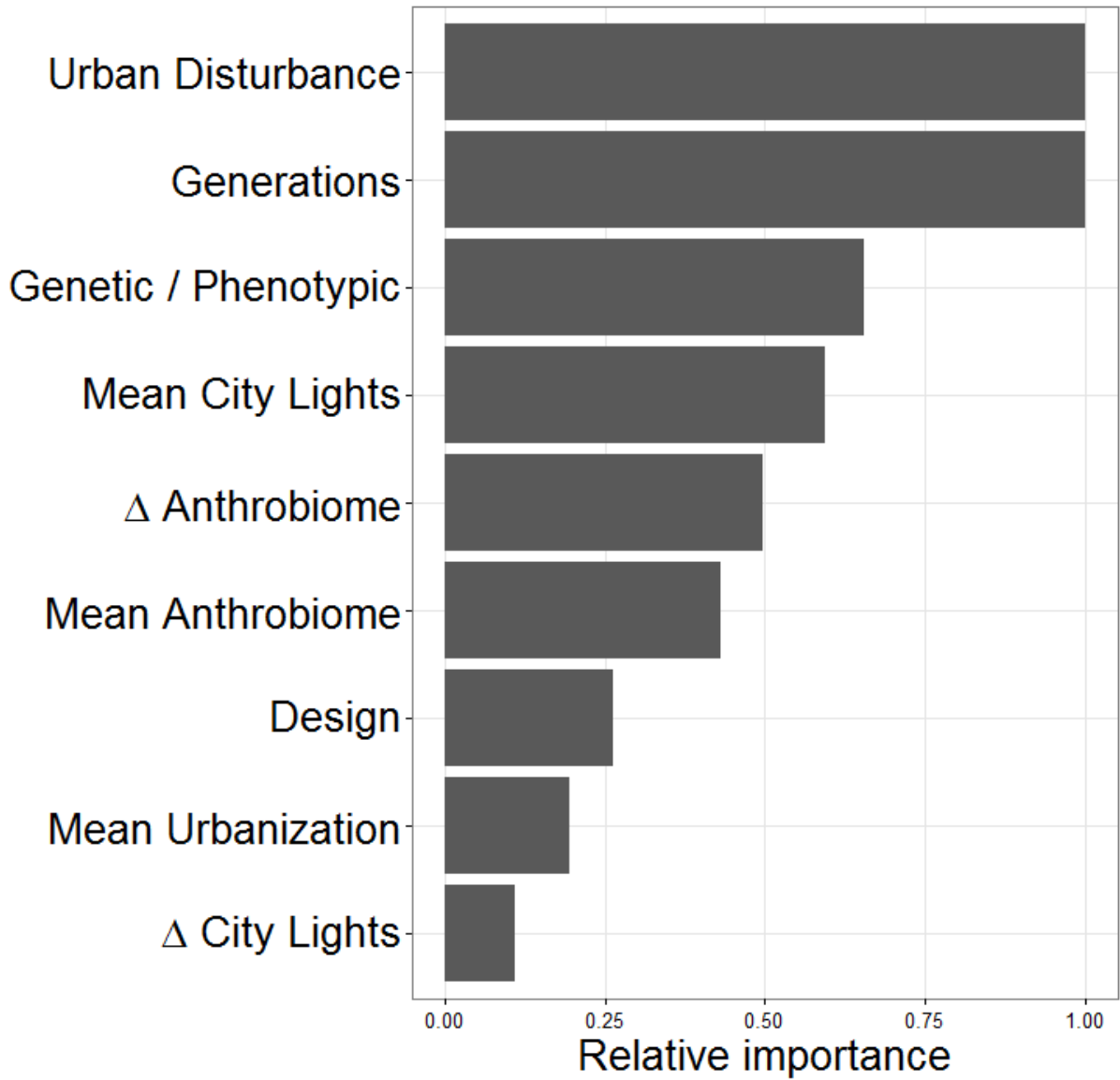


Figure S8 Relative importance of variables as inferred from multimodel inference.

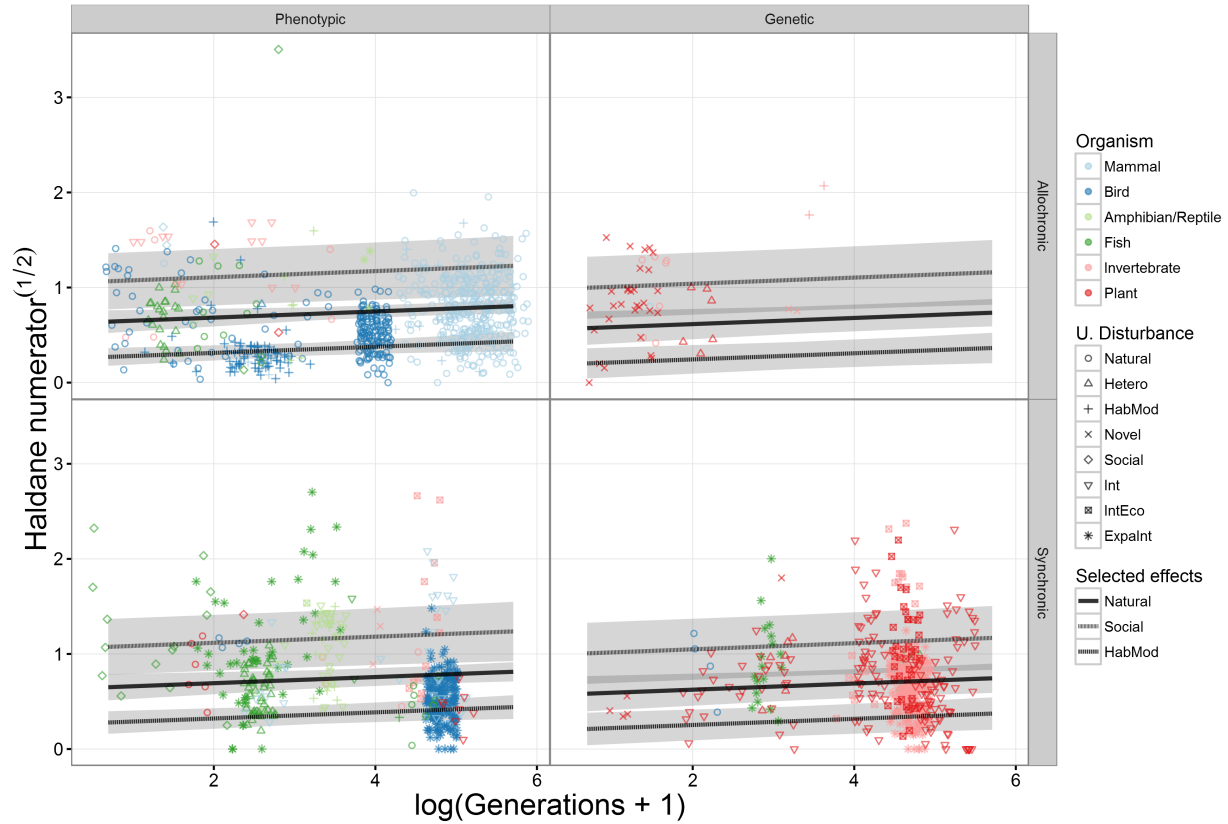


Figure S9 Multi-model predictions illustrating effect sizes, and distribution of observed phenotypic changes with respect to background variables: number of generations, study design (allochronic or synchronic), and genetic basis (genetic or phenotypic). *Urban Disturbance* (U. Disturbance) categories (symbols), and multi-model predictions for selected *Urban Disturbance* categories (regression lines and 95% confidence intervals) illustrate the gamut of expected effect sizes. The categories selected for display represent the range of expected effects due to *Urban Disturbance* (Table 1 and Figure 1, main article). Note the heterogeneous representation of predictor variable's categories in the data, and the relatively high effect sizes of *Urban Disturbance* compared to those of background variables, consistent with estimated variable relative importance (Fig S8). [For prediction, independent variables modeled but not shown were held statistically constant at mean values (continuous variables) or reference values (categorical variables). Data points were jittered horizontally to minimize superposition in the x-axis, hence the displayed number of generations is approximate.]

References

1. 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.
2. Pimentel D (1961) Animal Population Regulation by the Genetic Feed-Back Mechanism. *Am Nat* 95(881):65–79.
3. Schoener TW (2011) The Newest Synthesis: Understanding the Interplay of Evolutionary and Ecological Dynamics. *Science* 331(6016):426–429.
4. Matthews B, et al. (2011) Toward an integration of evolutionary biology and ecosystem science. *Ecol Lett* 14(7):690–701.
5. 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.
6. Alberti M (2015) Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol Evolut* 30(2):114–126.
7. United Nations, Department of Economic and Social Affairs, Population Division (2014) *World urbanization prospects: the 2014 revision : highlights (ST/ESA/SER.A/352)* (New York).
8. Seto KC, Gueneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *PNAS* 109(40):16083–16088.
9. Liu J, et al. (2013) Framing Sustainability in a Telecoupled World. *Ecol Soc* 18(2):26.
10. Marzluff JM, Angell T (2005) Cultural Coevolution: How the Human Bond with Crows and Ravens Extends Theory and Raises New Questions. *Journal of Ecological Anthropology* 9(1):69.
11. 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.
12. 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 University Press, Oxford, UK), p 131.
13. Hendry AP, Kinnison MT (1999) Perspective: The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* 53(6):1637–1653.
14. Kinnison MT, Hendry AP (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112:145–164.
15. Hendry AP, Farrugia TJ, Kinnison MT (2008) Human influences on rates of phenotypic change in wild animal populations. *Molec Ecol* 17(1):20–29.

16. Crispo E, et al. (2010) The evolution of phenotypic plasticity in response to anthropogenic disturbance. *Evol Ecol Res* 12(1):47–66.
17. 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.
18. Anderson DR (2008) *Model Based Inference in the Life Sciences: A Primer on Evidence* (Springer, New York ; London). 1st ed. 2008 edition.
19. Haldane J (1949) Suggestions as to Quantitative Measurement of Rates of Evolution. *Evolution* 3(1):51–56.
20. Nosil P, Harmon LJ, Seehausen O (2009) Ecological explanations for (incomplete) speciation. *Trends Ecol Evol* 24(3):145–156.
21. 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.
22. Mittelbach GG, et al. (2001) What is the observed relationship between species richness and productivity? *Ecology* 82(9):2381–2396.
23. Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. *Bioscience* 55(5):399–407.
24. 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. *Landscape Ecol* 23(10):1143–1155.
25. 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.
26. Pickett STA, et al. (2016) Dynamic heterogeneity: a framework to promote ecological integration and hypothesis generation in urban systems. *Urban Ecosyst*:1–14.
27. 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.
28. Groffman PM, et al. (2014) Ecological homogenization of urban USA. *Front Ecol Environ* 12(1):74–81.
29. Rebele F (1994) Urban Ecology and Special Features of Urban Ecosystems. *Global Ecol Biogeogr* 4(6):173–187.
30. 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.
31. 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).

32. 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.
33. Kille P, et al. (2013) DNA sequence variation and methylation in an arsenic tolerant earthworm population. *Soil Biol Biochem* 57:524–532.
34. Shenoy K, Crowley PH (2011) Endocrine disruption of male mating signals: ecological and evolutionary implications. *Funct Ecol* 25(3):433–448.
35. Bettencourt LMA (2013) The Origins of Scaling in Cities. *Science* 340(6139):1438–1441.
36. Clucas B, Marzluff JM (2012) Attitudes and actions toward birds in urban areas: Human cultural differences influence bird behavior. *Auk* 129(1):8–16.
37. Carroll SP, et al. (2014) Applying evolutionary biology to address global challenges. *Science* 346(6207):1245993.
38. Chislock MF, Sarnelle O, Jernigan LM, Wilson AE (2013) Do high concentrations of microcystin prevent Daphnia control of phytoplankton? *Water Research* 47(6):1961–1970.
39. 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.
40. Thrall PH, et al. (2011) Evolution in agriculture: the application of evolutionary approaches to the management of biotic interactions in agro-ecosystems. *Evolutionary Applications* 4(2):200–215.
41. McMahan RF (1976) Effluent-induced interpopulation variation in the thermal tolerance of *Physa virgata* Gould. *Comp Biochem Physiol A Comp Physiol* 55(1):23–28.
42. Al-Hiyaly 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.
43. 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.
44. Trussell GC, Smith LD (2000) Induced defenses in response to an invading crab predator: An explanation of historical and geographic phenotypic change. *P Natl Acad Sci-Biol* 97(5):2123–2127.
45. McGraw JB (2001) Evidence for decline in stature of American ginseng plants from herbarium specimens. *Biol Conserv* 98(1):25–32.
46. 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.
47. Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *PNAS* 104(4):1278–1282.

48. Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *P Roy Soc Lond B Bio* 270(1523):1467–1471.
49. Odling-Smee FJ, Laland KN, Feldman MW (2003) *Niche construction: the neglected process in evolution* (Princeton University Press, Princeton).
50. Bouma TJ, Vries MBD, Herman PMJ (2010) Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. *Ecology* 91(9):2696–2704.
51. Marzluff JM (2012) Urban Evolutionary Ecology. *Urban Bird Ecology and Conservation*, eds Lepczyk CA, Warren PS (University of California Press), pp 286–308.
52. Zhou Y, et al. (2015) A global map of urban extent from nightlights. *Environ Res Lett* 10(5):054011.
53. Zhou Y, et al. (2014) A cluster-based method to map urban area from DMSP/OLS nightlights. *Remote Sensing of Environment* 147:173–185.
54. Ellis EC, Ramankutty N (2008) Putting people in the map: anthropogenic biomes of the world. *Front Ecol Environ* 6(8):439–447.
55. 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].
56. 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].
57. Burnham KP, Anderson DR (2003) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, New York). 2nd edition.
58. Zuur AF ed. (2009) *Mixed effects models and extensions in ecology with R* (Springer, New York, NY).