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

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

25 eco-evolution | urbanization | ecosystem function | sustainability
26

Introduction

28 Emerging evidence of phenotypic change on contemporary time-scales
29 challenges the assumption that evolution only occurs over hundreds or
30 thousands of years. Anthropogenic changes in ecological conditions can
31 drive evolutionary change in species traits that can alter ecosystem
32 function (1–3). However, the reciprocal and simultaneous outcomes of
33 such interactions have only begun to emerge (4). Despite increasing
34 evidence that humans are major drivers of micro-evolution, the role of
35 human activities in such dynamics is still unclear. Might human-driven
36 evolution lead to ecosystem change with consequences for human
37 wellbeing within contemporary time-scales (5, 6)?
38 To address this question, human-driven phenotypic change must
39 be considered in the context of global rapid urbanization. In 1950, 30
40 percent of the world's population lived in urban settlements (7). By 2014,
41 that figure had risen to 54 percent, and by 2050 it is expected to reach 66
42 percent (7). By 2030, urban land cover is forecast to increase by 1.2
43 million km^2, nearly tripling the global urban land area of 2000 and
44 potentially driving significant biodiversity loss (8). Urbanization drives
45 systemic changes to socio-ecological systems by accelerating rates of
46 interactions among people, multiplying connections among distant
47 places, and expanding the spatial scales and ecological consequences
48 of human activities to global levels (9).
49 A critical question for sustainability is whether, on an increasingly
50 urbanized planet, the expansion and patterns of urban environments
51 accelerate the evolution of ecologically relevant traits with potential
52 impacts on urban populations via basic ecosystem services such as food

53 production, carbon sequestration, and human health (e.g. infectious
54 diseases). In cities, subtle and perhaps not so subtle eco-evolutionary
55 changes are occurring at an unprecedented pace. Humans challenge the
56 phenotypic, genetic, and cultural makeup of species on the planet by
57 changing the fitness landscapes on which they evolve. Examples of
58 contemporary evolution (sometimes called rapid evolution) associated
59 with urbanization have been documented for many species (1, 5, 6, 10).
60 This paper examines the mechanisms linking urban development
61 patterns to contemporary evolutionary changes. Through a meta-
62 analysis of experimental and observational studies that report >1600
63 phenotypic changes in many species of birds, fish, arthropods, mammals,
64 plants, and algae across multiple regions, we investigated the emergence
65 of distinct signatures of urban-driven evolutionary change. We
66 hypothesize that shifts in the physical and socio-economic structure and
67 function of large urban complexes can drive rapid evolution on many
68 species that play important roles in communities and ecosystems. Thus,
69 urbanization-driven phenotypic change may, in turn, impact critical
70 aspects of ecosystem function.
71 We ask two questions:
72 [1] Is there evidence of an urban signature of phenotypic change
73 beyond the established natural and anthropogenic signals, accelerating
74 rates of phenotypic change in species across multiple regions?
75 [2] What are the relative impacts of five different types of urban
76 disturbance: habitat modification, biotic interaction, heterogeneity, novel
77 disturbance, and social interaction?
78 Our hypothesis is grounded in the growing evidence that
79 urbanization is a major driver of contemporary evolution through several
80 mechanisms that operate simultaneously across multiple scales. Urban
81 development changes habitat structure (i.e., loss of forest cover and
82 connectivity) and processes (i.e., biogeochemical and nutrient cycling),
83 and it also modifies biotic interactions (i.e., predation) (6). Humans in
84 cities also mediate eco-evolutionary interactions by introducing novel
85 disturbances and altering habitat heterogeneity. Urban environments can
86 facilitate hybridization by bringing together species that were previously
87 reproductively isolated (11). They can also isolate populations through
88 habitat fragmentation (12). In addition to changes in the physical

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Significance Statement

Eco-evolutionary feedbacks on contemporary timescales were hypothesized over half a century ago, but only recently has evidence begun to emerge. The role that human activity plays in such dynamics is still unclear. Through a meta-analysis of experimental and observational studies that report >1600 phenotypic changes in species across regions and ecosystem types, we examine the evidence that the rate of phenotypic change has an urban signature. Our findings indicate greater phenotypic change in urbanizing systems compared to natural and non-urban anthropogenic systems. By explicitly linking urban development to trait changes that might affect ecosystem function, we provide insights into the potential eco-evolutionary implications for maintaining ecosystem function and the sustainability of human wellbeing.

template, humans in cities modify the availability of resources and their variability over time, buffering their effects on community structure (12). Complex interactions resulting from changes in habitat and biotic interactions coupled with emerging spatial and temporal patterns of resource availability might produce new evolutionary dynamics and feedbacks. Furthermore, what makes cities unique is the pace of change associated with increasing *social interactions* that amplify the direct and indirect impacts of human agency, both locally and in distant places (telecoupling). Understanding how urban-driven contemporary evolution affects ecosystem functions and services will provide new insights for maintaining biodiversity and achieving global urban sustainability.

Results

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

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

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

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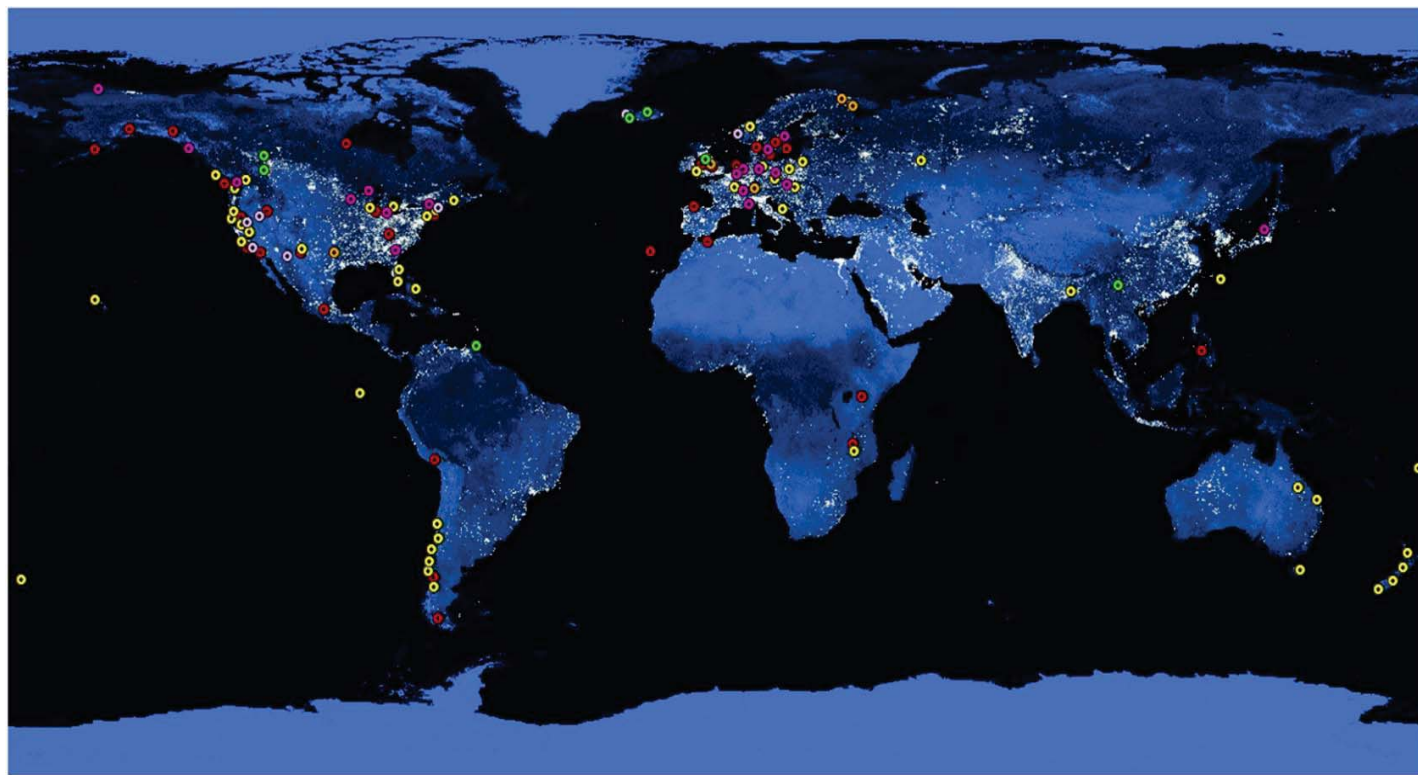
Urban Disturbance: ● Habitat Modification ◉ Heterogeneity ◉ Biotic Interaction ◉ Social Interaction ● Novel Disturbance

Other: ● Natural

Fig. 1. Global distribution of study systems of trait changes in wild populations. Symbols represent Urban Disturbances, wherein each study system is categorized according to its primary driver of phenotypic trait change. White regions represent City Lights as interpreted by Zhou et al. (2015) (53). Background of the Earth in 2012 from NASA: earthobservatory.nasa.gov/Features/NightLights/page3.php

153 set (512 models) was created by considering all combinations of the nine
154 explanatory variables in the fixed part of the GLMM (see Materials and
155 Methods and *SI p.10-15*). The random part of all models was held
156 constant, and included a random intercept per *Study System* to account
157 for nested data structure, and a previously selected variance function that
158 allowed the residual variance to scale with the expected response.
159 Phenotypic change (square-rooted) was the response variable,
160 measured as the absolute magnitude of phenotypic change standardized
161 by character variation, a quantity known as Haldane numerator (19).
162 Top-ranked models consistently included urban variables. For
163 example, the focal variables *Urban Disturbance*, *City Lights*, and
164 *Anthropogenic Biome* are prevalent in top-ranked models and in the 95%
165 confidence set, whereas, among background variables, *Generations* and
166 *GenPhen* were prevalent (Figure 2). Model-averaged partial regression
167 coefficients (incorporating model uncertainty) revealed several strong and
168 many weak effects (Table 1). Among urban-related variables, phenotypic
169 changes estimated from contrasts between urban vs. wild habitats (i.e.,
170 Δ *City Lights*) were higher than contrasts within either urban or wild
171 habitats. Mean *City Lights*, however, did not show a significant effect.
172 *Urbanization*, inferred from land-cover change during the last century
173 (mean *Urbanization*, with negative scores representing urbanization)
174 showed a trend with highest rates of phenotypic change in urbanizing
175 locations. This trend was not supported by the effect of contemporary land
176 cover (*Anthrobiome*). *Urban Disturbance* had many effects. For example,
177 social interactions, novel disturbances and introduction of predators,
178 prey, hosts, or competitors, were associated with relatively high
179 phenotypic change. Some effects were counterintuitive, e.g., habitat
180 modification was associated with relatively low phenotypic change. The
181 effects of *Urban Disturbance* were further illustrated by multimodel
182 predictions made while the effects of other variables were statistically held
183 constant (Figure 3). The range of effects attributed to Urban Disturbance
184 on multi-model predictions were substantial compared to those of
185 different combinations of background variables (*SI9*).
186
187 **Discussion**
188 Our results show a clear urban signal of phenotypic change and reveal
189 variable effects of urban disturbance mechanisms. *Urban Disturbance*

190 drives changes in species traits that may play significant roles in the
191 function of ecosystems and their stability, with significant consequences
192 for sustainability. The large urban effect might be due to the multiple
193 challenges that urbanization poses on adaptation. Multiple influences can
194 increase the total strength of selection on a trait, or the number of traits
195 under selection (20).

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

Parameter[a]	Estimate	Std. Error	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. – ExpaInt	0.005	0.09	0.059	0.953

198 Significance levels: P<0.001('***), P<0.01 (**), P < 0.05 (*), P < 0.1 (.)
199 [a] Abbreviations: Urban disturbance (U. Dist.), habitat modification
200 (HabMod), heterogeneity (Hetero), and subcategories of biotic
201 interaction: introduction (Int), introduction of predator/prey-
202 host/competition (IntEco), range expansion after introduction (ExpaInt).
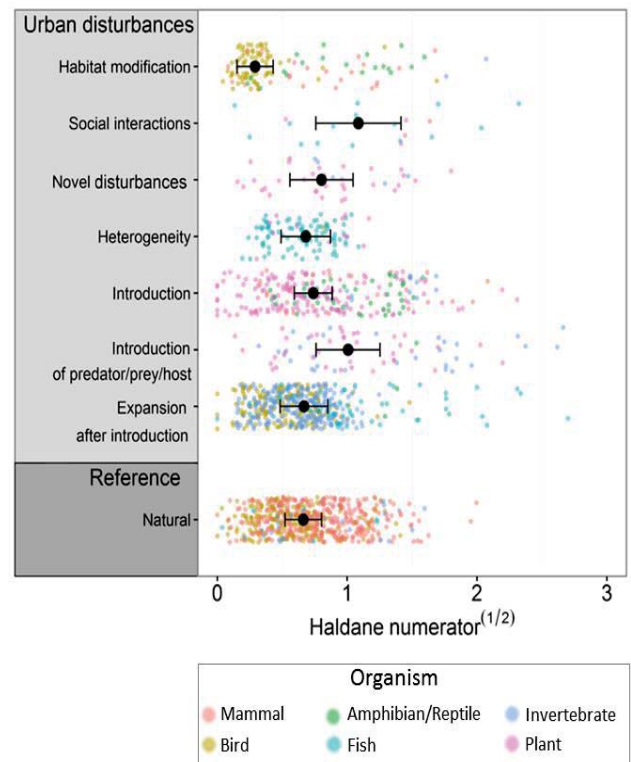
Figure 3. Multi-model predictions for *Urban Disturbance* categories. Some categories were associated with relatively high phenotypic change (i.e., Social Interactions and Introduction of predator/prey/host/ competitors) whereas others associated with background or even stable phenotypes (Habitat modification). Modelled, but not shown variables were held constant at means (continuous variables) or reference values (categorical variables).
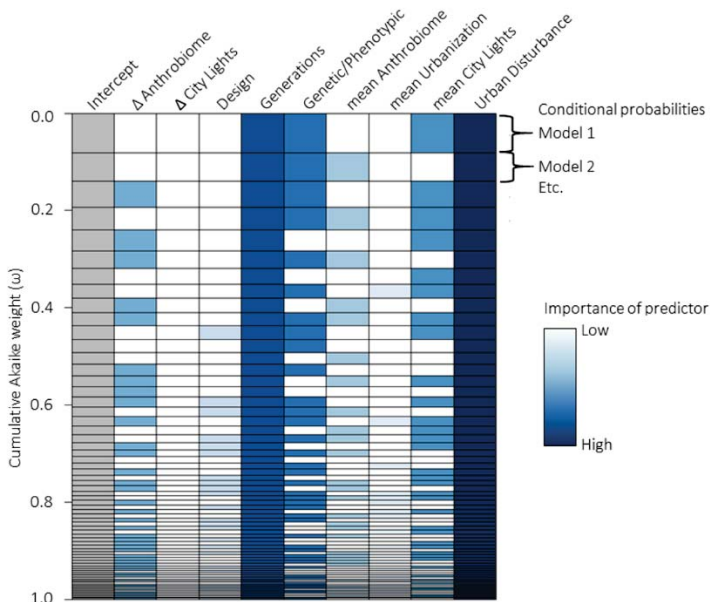

Figure. 2. Representation of the AICc model-selection table. Rows represent models sorted by decreasing empirical support (row height represents model probability conditional on the full model set). Predictor variables were shaded if included in a model. Saturation corresponded to estimated variable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

203 Urban Disturbance Mechanisms
204 *Urban Disturbance* represents coupled mechanisms through which urban
205 development affects natural processes and evolutionary dynamics. Model
206 predictions highlight three categories driving the urban signature: social
207 interactions, novel disturbances, and biotic interactions, specifically
208 introduction of predators, prey, hosts, and competitors. Anthropogenic
209 habitat modification was of lesser impact.

Habitat modification
211   Land cover conversion and loss of native habitat are major drivers
212 of contemporary evolution. Surprisingly, habitat modification driven by
213 anthropogenic change was not among the dominant drivers of higher
214 phenotypic change relative to the Natural context, suggesting that
215 globally, natural drivers of contemporary evolution might have
216 greater effects on phenotypic traits. In part, the effect of urban land cover
217 on phenotypic change is captured by *City Lights*. Yet urban-driven land
218 conversion affects species composition through subtle mechanisms not
219 captured by *City Lights*, but captured by our *Urban Disturbance* variable.
220 For example, changes in climate, artificial lighting, and availability of food
221 are principal drivers of change in the timing and duration of reproduction
222 in some bird species (21). Changes in productivity—the rate at which
223 energy flows through an ecosystem— might explain species diversity
224 patterns along the urban-to-rural gradient, though studies have produced
225 contradictory results. Changes in net primary production associated with
226 urban land-cover change affect faunal and plant species richness (22).

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

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

Novel Disturbance
262   Novel disturbance emerges as a dominant driver of phenotypic
263 change. Human-induced disturbances in urban environments maintain
264 urban habitats at an early successional stage (31). Such novel
265 disturbances alter resource availability, ecosystem productivity, and
266 species diversity (31). Cardinale et al. (2006) (32) suggested two ways
267 that disturbance can moderate relationships between biodiversity and
268 ecosystem functioning: it can increase the chance that diversity

269 generates unique system properties, and it can suppress the probability
270 of ecological processes being controlled by a single taxon. Urbanization
271 not only modifies existing disturbance regimes (e.g., fire and flood
272 management); it also creates novel disturbances including disrupted
273 dispersal pathways or stressors, eco-toxins and pollutants (33, 34).
274 Examples of phenotypic changes in response to new toxins include
275 earthworms' tolerance to metals (33) and changes in endocrine systems
276 of fish and birds (34).

Social Interactions
278   Perhaps the most significant quality that distinguishes cities is their
279 pace of change. Urbanization changes the dynamics of socio-ecological
280 interactions by increasing interactions among people (35), between
281 people and other species (36), and among distant places (9). Important
282 properties of cities of all sizes (i.e., gross domestic product) increase, on
283 average, faster than city population size (superlinearity). Increasing social
284 interactions accelerate environmental changes and human impact on
285 phenotypic traits via selective harvest (5).
286   Socio-economic shifts associated with urbanization can explain the
287 emergence of a detectable urban signature of evolutionary change. This
288 is also evident from the simultaneous effects of the *Urban Disturbance*
289 and *City Light variables*. The urban extent, regardless of boundary
290 definitions, only partially defines the extent of urban disturbances. City
291 functions depend on highly interconnected infrastructures and on flows of
292 material, energy, and information from both proximate regions (e.g., via
293 hydroelectric dams) and distant ones (e.g., via trade and
294 telecommunication). In urbanizing regions, distant human-natural
295 interactions are currently more prevalent and faster (9), challenging the
296 ability to disentangle urban vs. non-urban anthropogenic influences on
297 phenotypic traits.

Linking urban evolutionary change to ecosystem function
299   By explicitly linking urban development to traits that affect
300 ecosystem functions and services, we start to map the eco-evolutionary
301 implications of urban-driven phenotypic trait changes and identify existing
302 gaps in knowledge. The evolution of antibiotic resistance, pesticide
303 resistance, host-pathogen co-evolution, and evolution in response to
304 harvest and habitat change provide examples of the link between human-
305 driven evolution and sustainability (51). Urban environments provide the
306 context for many such interactions, bringing people in to contact with
307 novel pathogens, accelerating the spread of genes that confer resistance,
308 and generally selecting for traits that enhance the survival and
309 reproduction of wild organisms within human-built environments. When
310 this selection facilitates the survival of desirable species, it can have
311 important benefits for biodiversity, human health, and ecosystem
312 services. For example, evolution of *Daphnia* may help improve water
313 quality in the face of cultural eutrophication (37). However, adaptation can
314 also enable the survival and reproduction of species that reduce
315 biodiversity and human wellbeing. For example, evolution of pesticide
316 resistance in agriculture and antibiotic resistance in human medicine
317 represent critical threats to food security and human (38, 39).Thus,
318 evolution is instrumental to sustainability and should take on a prominent
319 role in the future of sustainability science.
320   Table 2 identifies examples of traits for which there is evidence of
321 evolutionary response to environmental changes driven by urbanization.
322 The evolution of traits that control ecosystem processes could lead to
323 significant changes in ecosystem functions (40). For example, primary
324 productivity is associated with consumers' traits that regulate their
325 demands for resources. Evolution in such traits can affect nutrient cycling
326 and ultimately the magnitude and spatial distribution of primary
327 production (4). Seed dispersers have a significant impact on plant
328 diversity and their functional roles in urban ecosystems. A great diversity
329 of organisms modify the physical structure of estuarine and coastal
330 environments, particularly dune and marsh plants, mangroves,
331 seagrasses, kelps, and infauna (41). Evolution in ecosystem-engineering
332 traits has potential functional impacts on maintaining the stability and
333 resilience (e.g., flood control) of coastal cities and the capacity of cities to
334 adapt to climate change.

335 Table 2: Mapping urban-driven phenotypic trait change to ecosystem function. Documented phenotypic trait changes, urban drivers, and hypothesized
336 eco-evolutionary feedback mechanisms.

Urban Signatures		Phenotypic trait	Eco-evolutionary feedback		Ref.
Urban Disturbance	*Mechanism*	**Physiological**	Ecosystem function	Feedback mechanism	
Novel	Exposure to effluent and associated extreme heat from a steam-electric plant	Mean heat coma temperature (thermal tolerance) in freshwater snails *(Physa virgata)*	Biodiversity	New 'physiological races' Colonization	(42)
Habitat modification	Anthropogenic acidification (pollution) of lake habitats	Survival in acidic conditions in moor frogs (*Rana arvalis*)	Biodiversity Nutrient cycling	Colonization Life history changes	(21)
Novel	Electricity pylons create novel habitats characterized by high levels of zinc	Zinc tolerance in plants: *Agrostis capillaris, Agrostis stolonifera, etc.*	Primary productivity Biodiversity	Consumer-resource dynamics	(43)
		Morphological			
Hetero-geneity	Hydrological connectivity altered via a fish ladder	Body size in brown trout (*Salmo trutta*)	Nutrient cycling	Life history changes	(44)
Biotic interaction	Invasion of a molluskivorous crab (*Carcinus maenas*)	Shell thickness (mm) in periwinkle snail (*Littorina obtusta*)	Biotic control	Trophic interactions	(45)
Social Interaction	Long-term selective harvesting of a medicinal plant	Size of American ginseng plants (*Panax quinquefolius*)	Primary productivity Biodiversity	Consumer-resource dynamics	(46)
		Behavioral			
Biotic interaction	Introduction (translocation) of animals to a predator-free island	Antipredator behavior in multiple species of marsupials	Nutrient cycling	Allocation of time to foraging vs. vigilance	(47)
		Phenological/Life History			
Hetero-geneity	Temporal heterogeneity in water availability (drought)	Flowering time in Field mustard (*Brassica rapa*)	Primary production	Consumer-resource dynamics	(48)
Habitat modification	Global warming	Seasonal onset of reproduction in 65 species of migratory birds	Biodiversity Biotic control	Colonization Novel competition	(49)

337

Conclusions

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

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

Materials and Methods

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, eco-evolutionary, anthropogenic change, urban disturbances, and system stability). Studies were screened for eligibility (see *Database filtering in SI*), and, if selected, phenotypic rates were extracted (see *Statistical analyses*) and classified according to qualities of the study system including ecological and anthropogenic contexts (5). Each row corresponded to one phenotypic change rate estimate and associated contextual attributes including type of study: *allochronic* for longitudinal studies, or *synchronic* for cross-sectional studies comparing samples obtained synchronously from populations derived from a common ancestral population. Rates were classified according to if phenotypic change could be attributed to quantitative genetic effects (*Genetic*), or could not be distinguished from phenotypic plasticity (*Phenotypic*).

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

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

Urban Disturbance classification and geo-referencing

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

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

Statistical analyses

We used an information-theoretic approach to rank statistical models and conduct multimodel inference, based on AICc (57)(61, 23). AICc favors model fit (minimizing

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

$$H^{(1/2)}_{(i)} = \alpha_{j(i)} + \beta \, \mathcal{X}_i + \mathcal{E}_i$$
$$\alpha_j \sim N(\mu, \sigma^2\alpha)$$
$$\mathcal{E} \sim N(0, f(\gamma))$$

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 $\mathcal{X}$, and $\mathcal{E}$, the residual error with variance γ, which was modelled 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} an exponent of absolute fitted values by stratum (2.0754 for genetic; 1.2376 for phenotypic). Hence, the chosen residual variance increased exponentially with fitted values, and slightly more so in genetic than phenotypic rates (SI, p. 10-15).

We used exploratory 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. 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. All models were fitted through maximum likelihood (ML) in the R package nlme (58). Models were ranked according to decreasing values of AICc (59), and further evaluated using standard methods after re-fitting through REML estimation (60). Predictor variable relative importance was calculated by the sum of the Akaike weights of all models containing a particular predictor variable. Similarly, model-averaged partial regression coefficients were Akaike-weighted averages of coefficients from all models containing a particular term (18). Model ranking and inference was conducted in the R package MuMIn v1.15.6 (57) (SI, p.10-15).

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