

1 **A framework to assess evolutionary responses to anthropogenic light and sound**

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24 **Keywords**

25 Light at night; anthropogenic noise; signalling; circadian rhythms; phenology; masking

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28 **Abstract**

29 Human activities have caused a near-ubiquitous and evolutionarily-unprecedented increase in

30 environmental sound levels and artificial night lighting. These stimuli reorganize communities

31 by interfering with species-specific perception of time cues, habitat features, and auditory and

32 visual signals. Rapid evolutionary changes could occur in response to light and noise, given their

33 magnitude, geographical extent, and degree to which they represent unprecedented

34 environmental conditions. We present a framework for investigating anthropogenic light and

35 noise as agents of selection, and as drivers of other evolutionary processes, to influence a range

36 of behavioural and physiological traits, such as phenological characters and sensory and

37 signalling systems. In this context, opportunities abound for understanding contemporary and

38 rapid evolution in response to human-caused environmental change.

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45 **Global changes in distribution of anthropogenic light and sound**

46 Worldwide human population growth dramatically influences organisms through urbanization,
47 industrialization, and transportation infrastructure [1]. The environmental disruption associated
48 with the exponential increase in human populations has led to extinction, altered community
49 structure, and degraded ecosystem function [1]. Pollution is among the key aspects of human-
50 induced rapid environmental change. Anthropogenic noise and artificial light are sensory
51 pollutants that have increased over recent decades, and pose a global environmental challenge in
52 terrestrial [2] and aquatic environments [3]. In 2001 approximately 40% of the world population
53 lived in areas that never experienced sub-moonlight illuminance [4]. Baseline night light levels
54 are increased by skylight, artificial light scattered by the atmosphere back towards the ground.
55 The overcast night sky radiance in urban areas has been found to be as much as four orders of
56 magnitude larger than in natural settings (Figure 1)[5]. Similarly, increased noise levels affect a
57 sizable proportion of the human population. In Europe for instance, 65% of the population is
58 exposed to ambient sound levels exceeding 55 dB(A) [6], roughly equivalent to constant rainfall.
59 Of the land in the contiguous U.S., 88% is estimated to experience elevated sound levels from
60 anthropogenic noise (Figure 1)[7]. These effects are not limited to terrestrial environments;
61 ocean noise levels are estimated to have increased by 12 decibels (an ~16-fold increase in sound
62 intensity) in the past few decades from commercial shipping alone [8], while an estimated 22%
63 of the global coastline is exposed to artificial light [3] and many offshore coral reefs are
64 chronically exposed to artificial lighting from cities, fishing boats, and hydrocarbon extraction
65 [9].

66 The changes in light at night and noise levels are occurring on a global scale similar to
67 well-recognized ecological and evolutionary forces such as land cover and climate change. In

68 parallel with research involving climate change [10], much of our understanding of organismal
69 response to noise and light is restricted to short-term behavioural reactions. Organismal
70 responses might be associated with tolerance to these stimuli in terms of habitat use [11,12], or
71 include shifts to quieter and darker areas [13,14]. Although organisms have responded to land
72 cover changes and climatic variability throughout history [10], the levels of night lighting and
73 noise now experienced are unprecedented in the evolutionary record. The rapid rise of these
74 novel stimuli could decrease the likelihood that organisms possess the genetic variance to adapt
75 to the altered environmental conditions.

76 Exposure to anthropogenic noise and artificial light can negatively affect the primary
77 sensory modalities by which most animals interact with their environment. Visual and auditory
78 systems mediate essential behaviours, including foraging, predator avoidance, territory defence,
79 and mating decisions [15]. When anthropogenic noise and light disrupt sensory systems, we
80 expect a cascade of effects on behaviours and associated life history traits. Light, for example,
81 plays a key role in modulating the circadian rhythms of both invertebrates and vertebrates, and
82 influences longer-term phenological responses [16]. Elevated light at night can reduce fitness
83 through immunosuppression [17] and alter reproductive physiology [18]. In terms of sound
84 stimuli, masking of acoustic cues is a mechanism by which noise affects animals [11]. This has
85 been studied in the context of songbird communication [12], yet masking can also influence
86 perceived risk due to impaired acoustic surveillance [19]. Other factors, such as distraction of an
87 animal's finite attention [17], have the potential to alter a variety of behaviours and traits.

88 Mounting evidence suggests that noise and night lighting have strong ecological
89 consequences [2,20], yet we know little about how these stimuli can drive evolutionary
90 responses. Here, we argue that evolutionary responses to these stimuli are highly likely and

91 propose a framework to guide future research (Figure 2), particularly as current studies rarely
92 distinguish between behavioural flexibility, developmental plasticity, or heritable genetic
93 responses. We describe how observed and hypothesized responses to these stimuli by individuals
94 and populations are linked through various mechanisms to evolutionary outcomes. Specifically,
95 we use a reaction-norm approach to show how researchers can investigate light and sound-
96 derived evolutionary responses. We then discuss how known behavioural and developmental
97 responses could contribute to evolutionary change.

98 **Status of research on anthropogenic light and sound in ecology**

99 Night lighting and noise are highly correlated in many landscapes (e.g., [21]). It is critical to
100 understand whether the selective pressures these stimuli exert are additive, synergistic (Figure 2),
101 or if they mitigate one another. Few studies have examined the influence of each simultaneously
102 (e.g., [21]). In one study, flashing lights combined with boat motor noise suppressed antipredator
103 behaviour in hermit crabs (*Coenobita clypeatus*) more so than noise alone [22]. Future research
104 should quantify both light and sound simultaneously in the same population. Existing research
105 has largely focused on these stimuli in isolation, so we briefly summarize the research status of
106 each separately.

107 *Anthropogenic sound as a potential selection pressure*

108 Noise can alter physiology, behaviour (communication, foraging, vigilance), and population-
109 level metrics such as abundance and density [11]; limited work suggests community-level effects
110 [23]. Most studies have been conducted over short time periods, and underlying mechanisms are
111 rarely elucidated. Francis and Barber [11] proposed a framework for understanding and
112 predicting behavioural responses and the likely fitness consequences in terms of both acute and
113 chronic noise exposure. Despite these steps towards an understanding of the ecological outcomes

114 of noise, it is unclear to what extent the documented outcomes represent evolutionary changes.
115 Similar to current challenges in understanding tolerance to climate change [10], a central
116 question is whether coping mechanisms among populations that persist in noisy environments
117 reflect behavioural flexibility, developmental plasticity, or microevolutionary responses. Some
118 recent evidence points to short-term behavioural responses [24], but it is unclear whether this
119 might be linked to microevolutionary responses that simply have not received attention (see
120 below).

121 *Anthropogenic light as a potential selection pressure*
122 The crucial role light plays in the regulation of physiology [25] and species interactions [26] has
123 been well studied, yet widespread effects of artificial light have received limited research
124 attention the past decade, starting with Longcore and Rich [27,28]. Until then, most research had
125 focused on documenting large-scale mortality events resulting from the attraction and
126 disorientation of animals (e.g., turtles and birds) by artificial lighting [28]. Research in the last
127 decade, however, have involved numerous biological responses [3,20], including effects of light
128 on physiology [17], reproduction [29], foraging [30], movement [31], communication [32], and
129 community ecology [33]. In addition to the range of biological responses, studies are now
130 beginning to consider effects from specific light spectra [34]. As with noise pollution,
131 evolutionary implications are largely understudied. One intriguing exception is a study of
132 nocturnal orb-web spiders, which demonstrated that webs were preferentially built in areas that
133 were artificially lit and, importantly, that the behaviour had a heritable basis [35].

134 *From proximate to ultimate effects of anthropogenic light and sound*
135 Organisms respond to anthropogenic light and noise, in a proximate sense, by way of two
136 mechanisms. One mechanism involves immediate adjustments to behaviour and physiology,

137 which we define as behavioural flexibility. The other mechanism operates through alterations of
138 developmental processes and gene expression that are influenced by local environmental
139 conditions as the organism develops its phenotype; this is developmental plasticity. Both forms
140 of variation can be visualized as a reaction norm (Figure 3a), which illustrates how phenotypic
141 expression varies across a range of environments. Specifically, developmental plasticity is
142 indicated by the slope of a single reaction norm and indicates whether a particular genotype
143 varies its ontogenetic production of a phenotype across an environmental gradient. Behavioural
144 flexibility can be visualized as error bars around a particular genotype (Figure 3a). In other
145 words, a genotype (e.g., an individual organism) can vary its behaviour within a particular level
146 of the environment, but it can also change its behaviour if it experiences a shift in the
147 environment.

148 Behaviourally flexible and developmentally plastic phenotypes resulting from noise and
149 light have largely been viewed as proximate responses to novel conditions [32,36]; however,
150 environmentally-induced phenotypes can become fixed through genetic accommodation and
151 assimilation [37], thus these responses could represent an initial step towards heritable change
152 (Figure 2c). Yet behavioural flexibility could also weaken selection. If the majority of genotypes
153 adjust behaviour in an adaptive direction there will generally be a decrease in the strength of
154 selection, because many genotypes will experience relatively enhanced fitness. Considerable
155 evidence has amassed for behaviourally flexible responses to alterations of the light and sound
156 environment (reviewed above). Studies should now take the next step to understand to what
157 degree these changes are linked, and potentially drive, heritable change.

158 Adaptive developmental plasticity can increase the strength of selection [38] because
159 genotypes capable of producing the higher fitness phenotypes will be selected for more strongly

160 than those unable to shift ontogeny in this adaptive direction. Even if most genotypes shift in an
161 adaptive direction, mechanisms of genetic accommodation could lead to positive selection [39].
162 There are few published studies involving developmentally plastic responses to noise and light
163 relative to evidence for immediate behavioural responses. Recent experiments using mice found
164 early life exposure to light at night can elevate anxiety behaviour in adulthood [40]. This is not
165 surprising given the extent to which photoperiod can impact the development of mice as a
166 function of altered circadian molecular rhythms, both during the perinatal [41] and postnatal
167 phases [42]. In birds, incubation under a long photoperiod results in smaller hatching size, a
168 fitness-related trait [43]. In terms of alteration of the acoustic environment, loud sounds can alter
169 the developmental trajectories of marine invertebrates [44], insects [36], and rodents [45].

170 Anthropogenic light and sound could also have heritable effects on developmental
171 trajectories, i.e., epigenetic effects (Figure 2c). Short-term changes in photoperiod can influence
172 gene expression profiles as well as DNA methylation, which might also be reversed by changes
173 in light regimes [46]. To our knowledge, researchers have yet to report possible epigenetic
174 influences of noise.

175 A central, yet relatively unexplored, question is whether the observed variation in a trait
176 responsive to noise or light is best explained by behavioural flexibility or developmental
177 plasticity. If developmental plasticity best explains the variation observed in nature, then it
178 increases opportunities for populations to respond in evolutionary ways. To assess this
179 evolutionary potential, information about the heritability of focal response traits must be
180 collected in the field as the environment is changing (Box 1). Understanding the heritability of
181 traits and the intensity and direction of selection as they occur in the field would allow prediction
182 of evolutionary outcomes for populations as well as understanding of current levels of

183 adaptation. Such research must address the complexities of selecting appropriate measurement
184 techniques, equipment, measurement precision, and units for characterization of light and sound
185 environments (Box 2).

186

187 **Potential microevolutionary responses**

188 Adaptive responses to anthropogenic light and sound require 1) a heritable response in the
189 population (e.g., mating calls); 2) a mechanism that alters gene frequencies from one generation
190 to the next (e.g., female preference for a specific call frequency); and 3) evidence that changes in
191 the light and or sound regime are causal agents driving the relationship the between heritable
192 response and the change in gene frequency in the population (e.g., a novel sound changes female
193 preference, which in turn drives changes in call structure). We briefly review additional
194 conditions for evolutionary change with respect to the four most commonly recognized forces of
195 evolution: selection, gene flow, drift, and mutation. These four mechanisms can operate
196 concurrently on the same population in environments influenced by light and noise.

197 *Sensory stimuli as drivers of selection*

198 Artificial light and noise can influence survival [28] and reproduction [32,47] of several animal
199 taxa. Numerous traits are associated with or depend upon animals' sensory systems; thus
200 evolutionary responses to these sensory stimuli will likely carry over to additional life history
201 traits. For example, both sound and light stimuli alter the configuration of communication
202 systems [15], which could influence other behavioural (e.g., agonistic interactions, mate choice,
203 vigilance, foraging efficiency), morphological (reception and production), and physiological
204 traits (e.g., stress hormone, immune function, metabolism).

205 Substantial evidence indicates that anthropogenic noise and light stimuli elicit phenotypic
206 responses (Table 1). Two traits with moderate heritability and phenotypic change are bird song
207 and circadian rhythms. Birdsong in noisy habitats, for example, can have altered structure,
208 timing, amplitude, and frequency parameters [12]. Some components of song production are
209 heritable, such as vocal processing regions of the brain [48] and beak morphology [49].
210 Interpretation of these observations, however, are complicated by the fact that the syntax and
211 note structure of bird song is learned in most of the species studied [50], confounding field
212 estimates of heritability. Furthermore, several studies demonstrate that some vocal adjustments
213 in response to noise are likely the result of immediate behavioural flexibility and not adaptive
214 change [24]. It is possible that this behavioural flexibility could still be a leader for evolutionary
215 change (Figure 2c). We posit that birdsong remains a likely trait under selection by
216 anthropogenic sensory stimuli and that the use of cross-fostering experiments in the laboratory
217 paired with field manipulations could prove a powerful approach to unveiling the strength of
218 noise as a selective agent.

219 Stronger evidence for adaptive change comes from altered light regimes. Circadian
220 rhythms are likely targets of selection because they are ubiquitous in almost all organisms and
221 synchronize to the external environment, with light as the primary *zeitgeber*. Although the
222 molecular basis of circadian clocks is highly conserved across taxa [16], heritable variation in
223 circadian rhythms is found within populations [51]. In the great tit (*Parus major*), for example,
224 circadian period length can be highly heritable ($h^2 = 0.86$) and in relatively closely related blue
225 tits (*Cyanistes caeruleus*), males that sing early have increased annual reproductive output by
226 increasing their extra-pair copulation success [32]. Because both tit species and several other
227 songbirds are known to begin singing earlier in the morning due to artificial light [32], artificial

228 night lighting might select for earlier chronotypes in birds. Indeed, Dominoni et al. [52]
229 demonstrated that European blackbird (*Turdus merula*) urban and rural populations differ in their
230 circadian rhythms and chronotypes as would be expected from the influence of artificial light.
231 Nevertheless, even in these cases it is difficult to distinguish the sources of variation: how much
232 is due to heritable change and how much to plasticity and flexibility? Traits that are likely under
233 selective pressure from anthropogenic light and sound should be studied using pedigree and
234 animal model studies in the field to directly quantify heritable variation and infer the remaining
235 flexibility and plasticity (Box 1). Critical experimental manipulations of sound and light stimuli
236 are also needed to unambiguously identify mechanisms; stimuli that represent relevant changes
237 that populations experience from various forms of human development should be used (Box 3).

238 *Sensory stimuli as drivers of gene flow*

239 Although gene flow is often interpreted as a homogenizer of connected populations, we propose
240 that differential dispersal and migration caused by changes in anthropogenic light and noise
241 could create biased gene flow. This could result in systematic genetic differences among
242 populations along light and sound level gradients. We know that the settlement, dispersal, and
243 migration patterns of many organisms are influenced by sound [53] and light [27,34]. We are
244 not, however, aware of investigations into whether these altered patterns of movement, and any
245 subsequent gene flow, have created genetic population differentiation. Disentangling genetic
246 differentiation due to noise or light versus other human-induced environmental changes
247 represents a promising avenue for research.

248 It is also possible that anthropogenic sensory stimuli create movement barriers and
249 reduces gene flow through habitat fragmentation. For example, birds that cannot communicate
250 effectively in noisy environments might not traverse this type of matrix. Some mammals tend to

251 avoid artificially lit environments, which would decrease connectivity [31]. A reduction in gene
252 flow could accelerate local adaptation to altered light and sound regimes but could also lead to a
253 loss of genetic variance in the long term.

254 *Sensory stimuli as drivers of genetic drift*

255 As we generally predict that increasing anthropogenic light and sound will fragment populations,
256 we expect that effective population size could be reduced in some localities, such as in many bird
257 populations in noisy areas [54]. This fragmentation could create a population bottleneck where
258 drift processes can have substantial consequences for populations, especially in terms of
259 decreased genetic variance. These ideas have yet to be explored empirically.

260 *Sensory stimuli as drivers of mutation*

261 Environmental stimuli can promote genetic mutations. Moderate and loud noise can increase
262 oxidative damage in several tissues of the body [55], which could induce mutations in the
263 germline of various taxa [56]. Increased noise could therefore directly induce germline mutations
264 and affect gene frequencies over time. Some evidence indicates that extremely loud sounds (90–
265 120 dB SPL) can lead to gross malformations of sperm in rats [57]. Few organisms experience
266 such extreme noise exposure levels in the wild; whether chronic exposure to less extreme noise
267 levels has similar effects represents a gap in our knowledge.

268 In parallel with the noise literature, there is laboratory evidence that light exposure,
269 especially in ultraviolet wavelengths, increases the probability of genetic mutations, including
270 within the germ lines of several taxa [58]. Thus, the mutagenic potential of anthropogenic
271 ultraviolet light, such as that produced by mercury vapor lamps, represents yet another area
272 requiring investigation. While alterations of mutation rates are likely not large enough to affect

273 rapid evolutionary change, we would be remiss to ignore the possible effects of anthropogenic
274 sensory stimuli on direct mutation.

275 **Macroevolutionary patterns**

276 The exploration of macroevolutionary patterns evident since the onset of industrial production of
277 light and sound should provide candidate systems for comparative analysis of population-level
278 and species-level responses.

279 *Recent divergence and phylogenetic trees*

280 A surge of research has predicted biodiversity scenarios for the near future based on
281 anthropogenic change [59]. This work has primarily focused on projecting species distributions
282 in relation to climate change. A similar approach should be applied to noise and light pollution
283 now that large-scale, fine-resolution spatial data on these stimuli are now available [7,60]. One
284 approach could include the construction of maps estimating background (pre-industrialization)
285 diversification and extinction rates for individual clades known or hypothesized to be influenced
286 by noise and light. Diversity data could then be used to determine whether contemporary rates
287 for species in particular sensory environments are different from background rates [61].

288 Phylogenies are useful for examining whether selection is occurring between sister
289 species (or species groups) that exhibit different sensitivities to light or sound. Studies on
290 mammals [62] and fish [63] have shown differential selection on visual transduction network
291 (VTN) genes in species from habitats with differing amounts of light. Genes associated with
292 light can be obtained from visual gene databases, including opsins and other genes in the VTN
293 [64]. Annotated genomes permit the identification of candidate genes and allow for the
294 determination of gene function.

295 *Differential extinction rates*

296 As celestial signals like the Milky Way disappear and night is replaced by extended twilight,
297 species specialized for night-time conditions are likely to be extirpated and species flexible in
298 their behaviour with respect to light will benefit [65]. Direct mortality from night lighting can be
299 significant at the population level. For example, fatal attraction to lights has resulted in the
300 extinction of at least two populations of the endangered giant water bug *Lethocerus deyrolli* [66].
301 Additionally, if not offset by rescue efforts, the attraction of young seabirds to urban lights could
302 extirpate Cory's shearwater *Calonectris diomedea* from the Azores [67]. Well-known declines of
303 nocturnal insects, such as moths [68], have been linked to artificial night lighting, yet it is
304 unclear whether this stimuli or other human-induced environmental changes are most
305 responsible. Declines among many taxa might be due to attraction and "entrainment" at lights, but
306 for some taxa, declines could also reflect interference with sexual signals (e.g., moths [29] or
307 fireflies). Indeed, firefly species richness is lower in areas characterized by 0.2 lux and higher
308 [69].

309 Noise also has potential to drive local extirpation and possibly extinction as evidenced by
310 diversity declines and avoidance of loud areas [13,14]. Among birds noise sensitivity is non-
311 random; species that experience the most vocalization interference from noise and those with
312 animal-based diets are most sensitive [54]. Because range size is often negatively correlated with
313 extinction risk [70], an urgent next-step will be to identify species with small ranges that have
314 undergone extensive transformations in altered sound and light levels. Doing so should prove
315 fruitful for evaluating the roles of impaired gene flow and drift in explaining evolutionary
316 responses to these novel stimuli.

317

318 Implications for conservation and biodiversity

319 The most immediate threat from anthropogenic noise and light is the loss of species that are
320 unable to adapt to their altered environment [11]. For example, disturbance from increased noise
321 and or light might convert some populations from sources to sinks through an inability to attract
322 mates or failed mating attempts [24], reduced physical fitness via elevated stress [71], or a
323 diminished ability to detect potential predators [11]. The loss of species might also have a
324 cascading effect on ecosystem function, such as altered rates and patterns of predation [14],
325 pollination and seed dispersal [23]. Despite mounting evidence that anthropogenic noise and
326 light negatively affects populations and communities, these stimuli are rarely considered in
327 conservation planning and restoration efforts.

328 Much less is known about how anthropogenic noise and light might influence evolution
329 and the potential implications for conservation. Behavioural responses to noise and light
330 exposure could result in the selection of maladaptive traits and the formation of evolutionary
331 traps [11]. In other cases, excessive noise and light can interfere with the acoustic and visual
332 communication used for mate selection, potentially resulting in the selection of lower quality
333 mates and reduced individual fitness [72]. It is also important to note that some species might
334 improve fitness through adaptation to louder and brighter environments, resulting in rapid
335 population increases and the emergence of a highly abundant pest species [73].

336 Evolution occurs on a timescale that is at odds with the immediacy of conservation
337 efforts. Stimuli that alter the intensity, duration, and cycles of natural sound and light
338 environments, however, have the potential to drive profound and rapid evolutionary change. As
339 anthropogenic changes to sound and light are so large relative to natural fluctuations, we propose
340 that human-induced light and sound might be particularly effective agents of selection.

341 Understanding how noise and light might drive selection, as we propose, is a priority for a world
342 that is, unfortunately, increasingly loud and bright.

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348

349 **Figure legends**

350

351 Figure 1. Increasing anthropogenic night lighting and sound levels represent a global
352 phenomenon that constitutes environmental changes unprecedented in the history of life on
353 Earth. **(A)** Europe at night. Areas colored blue are emitting an amount of light upwards that are
354 comparable to moonlight, pink areas are brighter than moonlight, and white areas are many times
355 brighter than moonlight. **(B)** Light is extremely heterogeneous at both landscape and local (few
356 meters) spatial scales. **(C)** Estimated sound levels (L_{50} SPL dB(A) re $20\mu\text{Pa}$) created by human
357 activities that exceed background levels created by natural sources [7]. **(D)** Temporal
358 heterogeneity in anthropogenic sounds as a 24-hr spectrogram, which illustrates acoustic energy
359 across the frequency spectrum for 24-hrs, with each row representing 2-hrs. Lighter colors reflect
360 higher sound levels. Brighter colors prominent in the fourth row (i.e., beginning at 6am) through
361 the final row display anthropogenic sounds from road traffic and aircraft in Grand Teton
362 National Park in late September of 2013. (A) Image and Data processing by NOAA's National
363 Geophysical Data Center, (B) courtesy Freie Universität Berlin & (C) modified from Mennitt et
364 al. [7]. Both (C) and (D) are courtesy of the U.S. National Parks Natural Sounds and Night Skies
365 Division.

366

367 Figure 2. Framework for evaluating how anthropogenic night lighting and sound can influence
368 behavioural, developmental, and evolutionary outcomes. **(A)** Anthropogenic light at night and
369 sound share many features relevant to animal sensory systems. Listed are only a few candidate
370 features of noise and light important to investigating the potential strength of these stimuli as
371 agents of ecological and evolutionary change, whether alone or combined given that these

372 stimuli often co-vary in many environments. See Francis & Barber [11] for a review of some of
373 these features. Because these stimuli can co-occur in many environments, we propose that
374 human alterations of light and sound can act synergistically on wildlife. **(B)** Effects of
375 anthropogenic sound and night at light are known or hypothesized to affect many levels of
376 biological organization, which could result in evolutionary change via different pathways, such
377 as selection, drift or epigenetic inheritance. Table 1 provides a more comprehensive list of
378 known and hypothesized ecological and evolutionary outcomes due to noise and light. **(C)**
379 Influences of anthropogenic sound and light at different levels of biological organization can
380 result in short-term behavioural flexibility, developmental plasticity, and microevolutionary
381 responses via different evolutionary forces (see Potential Microevolutionary Responses section)
382 and induce responses by individuals and populations over different spatial scales. Importantly,
383 shorter-term phenotypic responses could lead to genetic (evolutionary) change through processes
384 of genetic assimilation and accommodation, which could make evolved responses occur faster
385 or, alternatively, could weaken selection if all genotypes experience high fitness as a result of
386 sound or light-induced behavioural and developmental shifts.

387

388 Figure 3. **(A)** Example reaction norms of phenotypic responses to anthropogenic sound and light.
389 Each line represents the phenotype expressed by a different genotype in the population, across an
390 environmental gradient. The slope of the response represents the developmental plasticity of a
391 genotype. The error bars on each reaction norm represent behavioural flexibility as an individual
392 can alter their phenotype through behavioural mechanisms independently of developmental
393 plasticity. The distance between the lines at any given level of stimulus represents heritable
394 variation, as these are differences in phenotypic expression among the genotypes in the

395 population. **(B)** Behavioural and developmental responses to anthropogenic sound and light
396 could influence patterns of divergence (modified from Lema [74]. Black line denotes mean
397 phenotypic trait value and grey lines reflect the range of trait variation under natural light and
398 sound regimes. Anthropogenic sound or light could generate rapid phenotypic divergence by
399 triggering behavioural or developmental responses well outside of the range of variation in
400 environments without these stimuli (dashed horizontal line). Rapid phenotypic change via
401 developmental or behavioural mechanisms can occur when a population colonizes an
402 environment characterized by novel light and sound regimes or if these stimuli are rapidly
403 introduced to an existing population. These novel phenotypes (blue line = mean trait value, light
404 blue = range of expression) might then become canalized in the new environment (e.g., genetic
405 assimilation).

Table 1. Numerous traits are candidates for selection by light at night and anthropogenic noise and span behaviour, morphology and physiology, some of which are directly related to phenology. The sample list below identifies candidate traits by category and selective pressure (artificial night lighting and noise) and provides evidence, if available, for observed phenotypic changes and heritability estimates for each trait.

Trait Category	Selective Pressure	Candidate Traits	Phenotypic Change	Heritability estimates
Communication and behaviour	Acoustical environment can mask or interfere with vocal signals, or be timed to interfere with vocal signalling	Vocal signal features (frequency, timing, amplitude)	Sound level-dependent frequency use, increased amplitude [12]	Song control nuclei: HVC volume $h^2 = 0.38$, RA volume $h^2 = 0.72$ [48]
		Signal modality	Switch to emphasize visual cues in high noise [75]	Not reported
		Agonistic interactions	Males respond differently to urban songs [12]	Aggression, $h^2 = 0.10$ (20); exploratory behaviour, $h^2 = 0.54$ [76]
		Mate choice	Preference for low frequency songs erodes with urban noise [72]; noise decreases preference for own mate [77]	Not reported
		Vigilance	Increased vigilance behaviour in noise [78]	Vigilance, $h^2 = 0.08$ [79]
		Foraging efficiency	Successful foraging bouts decreased and foraging time increased near noisy roads [80]	Proportion of prey captured in neonates, $h^2 = 0.32\text{--}0.54$ [81]
		Learning and cognition	Reduced learning after noise exposure [55]	Learning in bees, $h^2 = 0.39\text{--}0.54$ [82]
		Sound production	Coupling of amplitude and frequency such that both increase in urban noise [83]	Beak length, depth, and width, $h^2 = 0.65\text{--}0.90$ [49]

	Rates and timing of signalling	Increased signalling at times without high noise [84]	Endogenous circadian period length, $h^2 = 0.86$ [51]
	Timing of dawn song	Advance of dawn song, altered attractiveness male birds [32]	Not reported
	Timing of reproduction	Advancement of reproductive physiology of blackbirds [18]	Not reported
Exposure to light at night around dawn and dusk, and to low light levels at night	Feeding behaviour	Increase of chick feeding behaviour in great tits [85]	Not reported
	Nest site choice	Avoidance of light at nest sites by godwits [86]	Not reported
	Reproduction	Alteration of mating behaviour in moths [29]	Not reported
	Calling and movement behaviour	Reduced advertisement call activity, less movement activity [87]	Not reported
	Emergence time	Delayed emergence time [88]	Not reported
	Daily timing of feeding behaviour	Switch to nocturnal feeding [30]	Not reported
Acoustical environment can mask or interfere with vocal signals		Sound reception	Individuals respond differently to attenuated versions of vocal signals [89]
Morphology	Eye size		Hearing loss, $h^2 = 0.36$ [90]
	Exposure to light at night	Body mass	Eye size, $h^2 \leq 0.5$ [91]
Physiology	Exposure to increased acoustical noise	Stress hormones	Elevated corticosterone levels [92]
		Metabolism	Corticosterone levels, $h^2 \leq 0.27$ [93] Increased oxidative damage in noise [55]
			Not reported

	Cardiovascular health	Increased occurrence of hypertension and cardiovascular disease in humans [94]	Not reported
	Stress hormones, melatonin	Reduced expression of melatonin, change of pattern of hormone expression [95]	As above
Exposure to low light levels at night	Timing of reproduction, moult	Early onset of gonadal growth, temporal organization of moult [18]	Not reported
	Immune system	Change of immune response to challenges: delayed-type hypersensitivity, induced fever, bactericide activity blood [17]	Not reported
	Pheromone release	Suppression of pheromone release	Not reported

1 **Text Boxes**

2

3 **Box 1. How to measure heritability in the field**

4 To estimate heritability in wild populations we need to disentangle the observed variation in a
5 trait between genetic and environmental components. Also, within the genetic variance it is often
6 useful to directly estimate the narrow-sense heritability, which tells us how much of variance is
7 due to additive genetic effects (of multiple loci influencing a complex quantitative trait), and is
8 estimated by comparing relatives with each other. In particular, we advocate for animal model
9 approaches to estimating heritability [96]. In such a technique, information about genetic
10 relatedness of individuals in populations is collected to construct pedigrees that are then analysed
11 using generalized linear model approaches that partition phenotypic variance among possible
12 genetic explanations. One of the advantages of this approach over others is that some statistical
13 models can use incomplete pedigrees that include quite distant relationships, making the methods
14 fairly amenable to estimating heritability from field population datasets [96]. Many of the traits
15 we propose could evolve in relation to altered anthropogenic light and sound are close to
16 Gaussian-distributed (Table 1), therefore it appears that maximum likelihood approaches to
17 estimating heritability through animal models could be most appropriate in many cases [97].

18

19 **Box 2. Measurement of light and sound: challenges and recommendations**

20 In contrast to scalar variables like temperature or concentration of a chemical substance, the
21 spectral and vector nature of both light and sound make measurement more challenging,
22 particularly in field settings. There are also many different units of measurement, which are
23 likely not familiar to many ecologists and evolutionary biologists (e.g. illuminance vs. spectral
24 radiance). Past studies have often opted to use a simple, inexpensive metric, but in many cases
25 wrong instrument choice can lead to incorrect conclusions. As an example, in many cases it
26 might not be the overall light or sound level that is important, but rather a signal-to-noise ratio.
27 In vision, for example, scenes with identical irradiance can have vastly different levels of
28 contrast and glare.

29 **Challenges**

- 30 • Range: Both light and sound vary over many orders of magnitude, changing on a
31 timescale of seconds to minutes. Sound is measured on a logarithmic scale, as is light in
32 astronomy.
- 33 • Direction of wave propagation: Animal responses usually depend not only on integrated
34 fluxes, but also directional information. Glare and contrast can be critical in artificially lit
35 scenes.
- 36 • Spectral weighting: human perception does not necessarily match animal perception, but
37 full spectral measurement is expensive and difficult.
- 38 • Short duration variations: Amplitude and frequency modulation might need to be
39 measured for sound, flicker could be important for artificial light.

- 40 • Location of measurement: Ideally, both noise and light exposure should be measured
41 directly on the target animal, although this can be expensive and time-consuming. If not
42 possible, then the measurement should be done as close as possible to the animal's core
43 area.

44 **Recommendations:**

- 45 • Tradeoffs must be assessed in the planning stage to find a measurement technique that is
46 appropriate to answer the question under investigation. Recording spectral information is
47 highly recommended. Tradeoffs are more acceptable in field experiments, where
48 conditions can be highly variable. Full spectral characterization should be standard in
49 laboratory studies [98].
- 50 • Instruments must have sufficient range and precision. Measurements at the edge of an
51 instrument's range provide insufficient information.
- 52 • It is likely unnecessary and unproductive to develop mastery in an outside discipline.
53 Find collaborators from outside of your field to provide advice and assistance in
54 measurement. Similar to consulting a statistician, experimental setup should be discussed
55 with a professional (e.g., a lighting or acoustical engineer).
- 56
- 57

58 **Box 3. Suitable study systems or potential traits under selection**

59 Numerous traits are potentially under selective pressure by anthropogenic light and sound (Table
60 1). The challenge is to actually show selection and microevolutionary responses. The relation
61 between traits and reproductive fitness is ideally studied experimentally via controlled treatments
62 to light and sound stimuli alone and combined in an otherwise unchanged environment. A good
63 approach is the assessment of genetic and phenotypic diversity in a species with discrete
64 populations in urban and natural areas. This can be studied directly in an integrated manner by
65 looking at morphology, behaviour, physiology and (single nucleotide) polymorphisms, and
66 connected selective sweeps. Yet areas exposed to novel noise and light regimes, such as urban
67 areas, are often influenced by many other environmental factors. A more powerful design is to
68 experimentally test individuals from populations in both environments in a new, controlled setup
69 for differences in responses to urban stimuli such as light and sound and focusing on candidate
70 genes linked to traits hypothesized to be under selection or by using genome scanning
71 approaches. Indeed, such “common garden” experiments have revealed important information on
72 differences between urban and wildland populations [99]. It is critical, however, to test whether
73 these differences persist in successive generations. Conducting such studies in the field or
74 laboratory will be challenging, especially for organisms that have low fecundity and are long-
75 lived. For these organisms, selection might only occur after considerable time or not at all given
76 that slower life histories could have lower evolutionary potential in the face of rapid
77 environmental change [100]. Nevertheless, numerous taxa with traits likely under selection by
78 anthropogenic sound and light and with higher evolutionary potential could be studied over
79 shorter timeframes (Table 1).

80
81

82 Glossary

83 Background extinction rates: pre-human rates of extinction outside of recognized mass extinction

84 events.

85 Background speciation rates: pre-human rates of speciation outside of the recovery period

86 following mass extinction events.

87 Behavioural Flexibility: Immediate adjustments of behaviour and physiology in response to

88 environmental conditions.

89 Developmental Plasticity: A single genotype's change in developmental trajectory and

90 phenotypic outcome in response to a different environmental condition.

91 Heritability: The proportion of phenotypic variance attributable to genetic variance.

92 Macroevolution: The study of patterns and processes of evolution that occur at or above the level

93 of species.

94 Microevolution: Change in allele frequencies in a population over time.

95 Reaction Norm: Depiction of the range of phenotypes expressed by a single genotype across

96 different environments.

97 Zeitgeber: Any external cue that entrains an organisms' biological rhythms to environmental

98 cycles.

99

100

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324
325

Figure 1

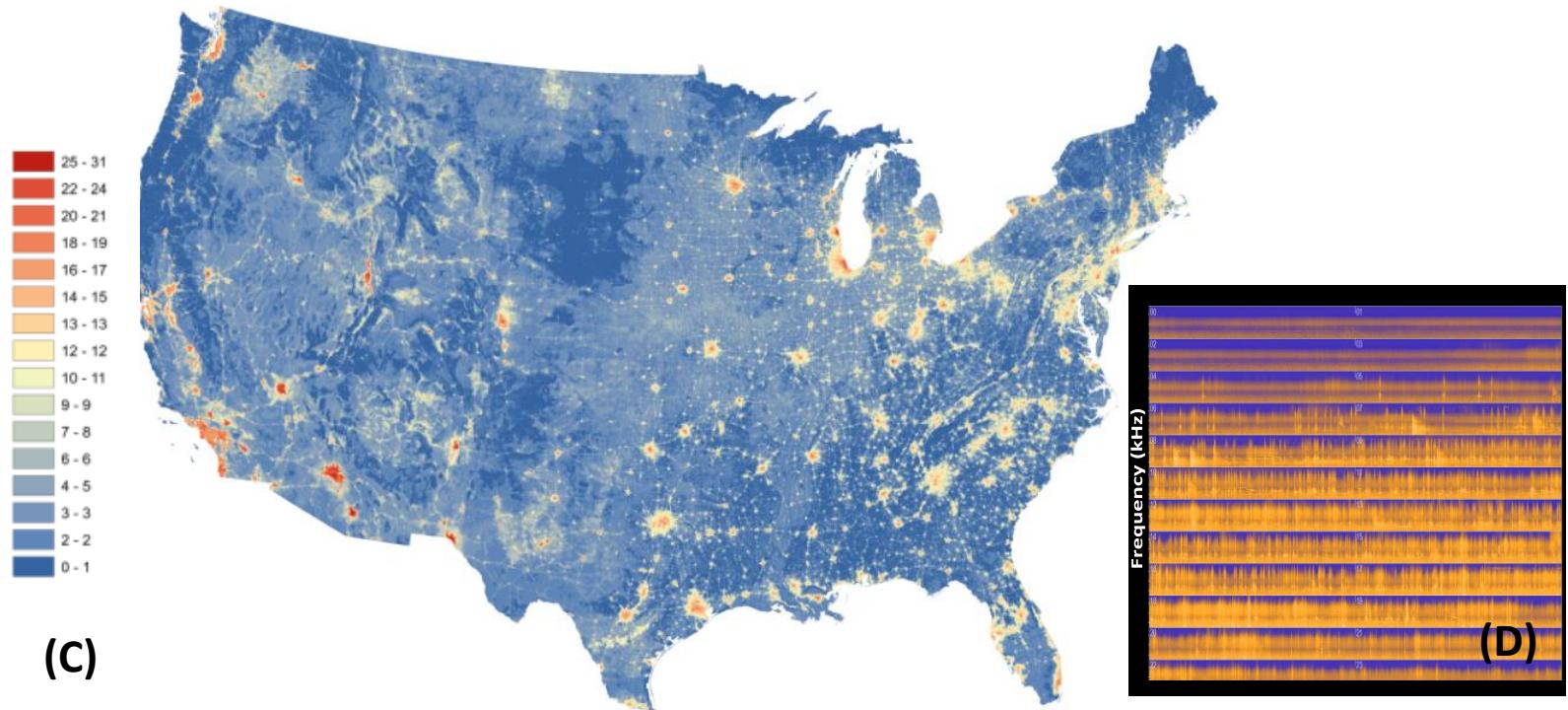
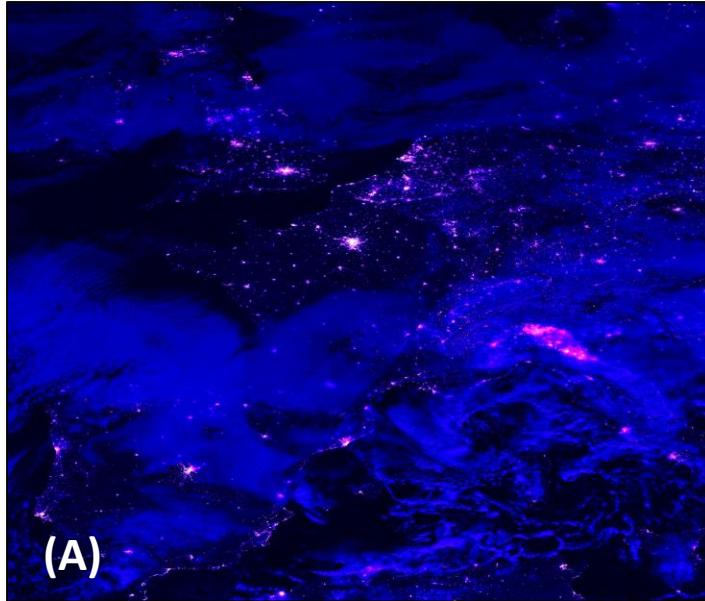


Figure 2

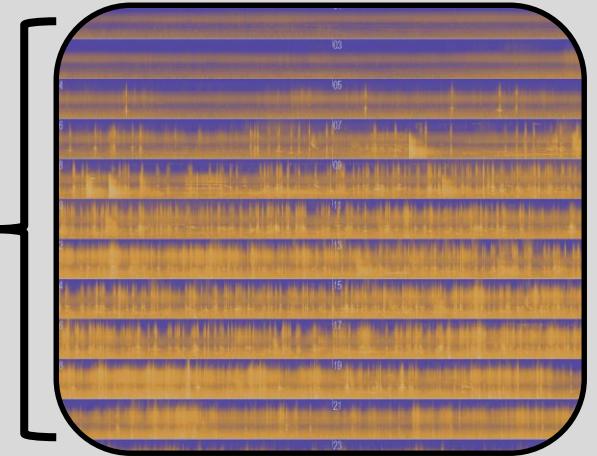
(A) Human-caused lighting



Combined effects among:

- Sensory system relevance
- Temporal overlap with key physiological and behavioral functions
- Duration, predictability, and intensity

Human-caused sounds



(B)



(C)

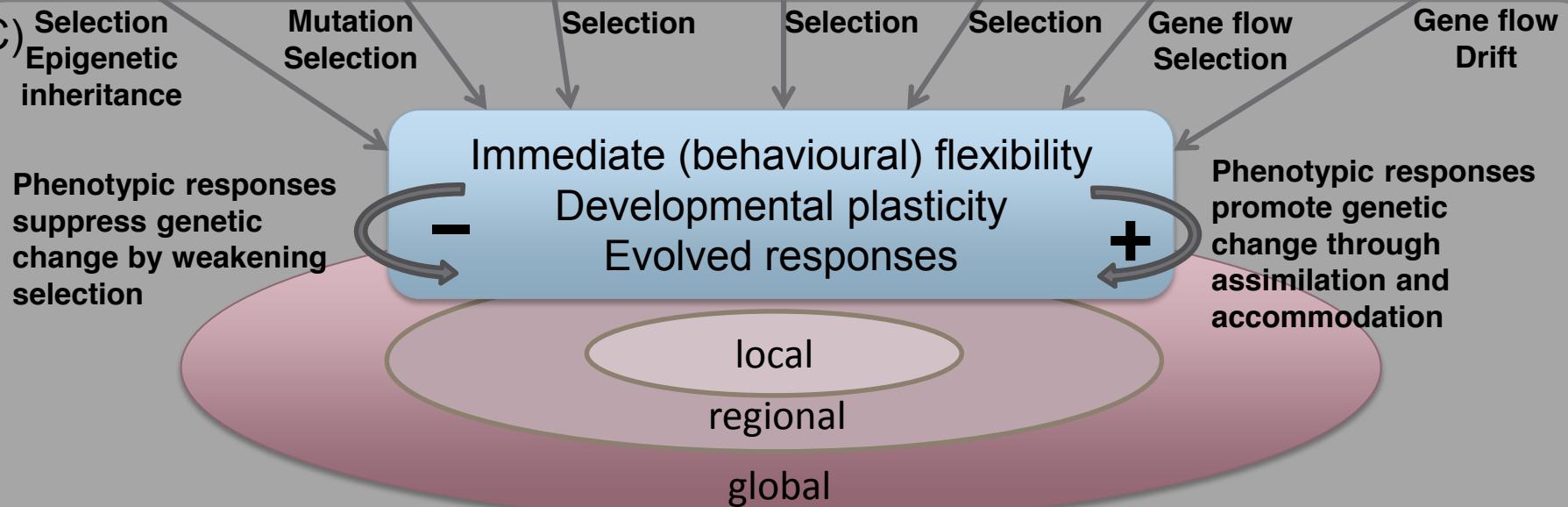


Figure 3

