

A framework to assess evolutionary responses to anthropogenic light and sound

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Human activities have caused a near-ubiquitous and evolutionarily-unprecedented increase in environmental sound levels and artificial night lighting. These stimuli reorganize communities by interfering with species-specific perception of time-cues, habitat features, and auditory and visual signals. Rapid evolutionary changes could occur in response to light and noise, given their magnitude, geographical extent, and degree to which they represent unprecedented environmental conditions. We present a framework for investigating anthropogenic light and noise as agents of selection, and as drivers of other evolutionary processes, to influence a range of behavioral and physiological traits such as phenological characters and sensory and signaling systems. In this context, opportunities abound for understanding contemporary and rapid evolution in response to human-caused environmental change.

Global changes in distribution of anthropogenic light and sound

Worldwide human population growth dramatically influences organisms through urbanization, industrialization, and transportation infrastructure [1]. The environmental

disruption associated with the exponential increase in human populations has led to extinction, altered community structure, and degraded ecosystem function [1]. Pollution is among the key aspects of human-induced rapid environmental change. Anthropogenic noise and artificial light are sensory pollutants that have increased over recent decades, and they pose a global environmental challenge to terrestrial [2] and aquatic environments [3]. In 2001 approximately 40% of the world population lived in areas that never experienced sub-moonlight illuminance [4]. Baseline night light levels are increased by skyglow, artificial light scattered by the atmosphere back towards the ground. The overcast night sky radiance in urban areas

Glossary

Background extinction rates: pre-human rates of extinction outside of recognized mass extinction events.

Background speciation rates: pre-human rates of speciation outside of the recovery period following mass extinction events.

Behavioral flexibility: immediate adjustments of behavior and physiology in response to environmental conditions.

Developmental plasticity: a change in developmental trajectory and phenotypic outcome of a single genotype in response to a different environmental condition.

Heritability: the proportion of phenotypic variance attributable to genetic variance.

Macroevolution: the study of patterns and processes of evolution that occur at or above the level of species.

Microevolution: change in allele frequencies in a population over time.

Reaction norm: depiction of the range of phenotypes expressed by a single genotype across different environments.

Zeitgeber: any external cue that entrains the biological rhythms of an organism to environmental cycles.

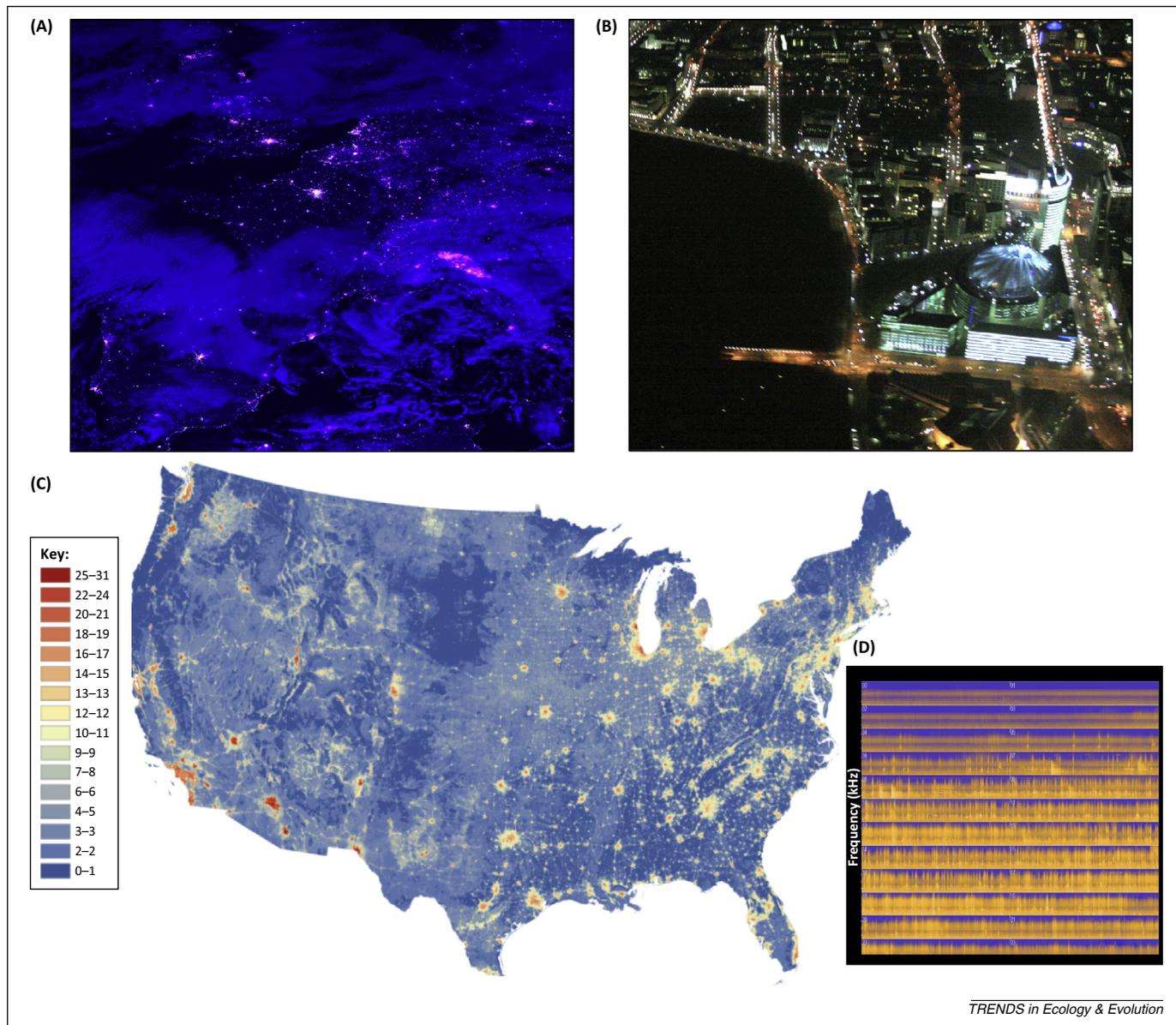
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Keywords: light at night; anthropogenic noise; signaling; circadian rhythms; phenology; masking.

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0169-5347/

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TRENDS in Ecology & Evolution

Figure 1. Increasing anthropogenic night lighting and sound levels represent a global phenomenon that constitutes environmental changes unprecedented in the history of life on Earth. **(A)** Europe at night. Areas colored blue are emitting an intensity of light upwards that is comparable to moonlight, pink areas are brighter than moonlight, and white areas are many times brighter than moonlight. **(B)** Light is extremely heterogeneous at both landscape and local (few meters) spatial scales. **(C)** Estimated sound levels (L50 SPL dB(A) re 20 μ Pa) created by human activities that exceed background levels created by natural sources [7]. **(D)** Temporal heterogeneity in anthropogenic sounds as a 24 h spectrogram, which illustrates acoustic energy across the frequency spectrum for 24 h, with each row representing 2 h. Lighter colors reflect higher sound levels. Brighter colors prominent in the fourth row (i.e., beginning at 06.00 h) through the final row display anthropogenic sounds from road traffic and aircraft in Grand Teton National Park in late September of 2013. (A) Image and Data processing by the National Oceanic and Atmospheric Administration (NOAA) National Geophysical Data Center, (B) courtesy Freie Universität Berlin, and (C) modified from Mennitt *et al.* [7]. Both (C) and (D) are courtesy of the US National Parks Natural Sounds and Night Skies Division. Abbreviations: dB(A), A-weighted decibels; L50, median SPL; re, reference pressure; SPL, sound pressure level.

has been found to be as much as four orders of magnitude larger than in natural settings (Figure 1) [5]. Similarly, increased noise levels affect a sizable proportion of the human population. In Europe, for instance, 65% of the population is exposed to ambient sound levels exceeding 55 dB(A) [6], roughly equivalent to constant rainfall. Of the land in the contiguous USA, 88% is estimated to experience elevated sound levels from anthropogenic noise (Figure 1) [7]. These effects are not limited to terrestrial environments; ocean noise levels are estimated to have increased by 12 decibels (an \sim 16-fold increase in sound intensity) in the past few decades from commercial shipping alone [8], while an estimated 22% of the global coastline is exposed to

artificial light [3], and many offshore coral reefs are chronically exposed to artificial lighting from cities, fishing boats, and hydrocarbon extraction [9].

The changes in light at night and noise levels are occurring on a global scale similar to well-recognized ecological and evolutionary forces such as land-cover and climate changes. In parallel with research involving climate change [10], much of our understanding of organismal response to noise and light is restricted to short-term behavioral reactions. Organismal responses might be associated with tolerance to these stimuli in terms of habitat use [11,12], or include shifts to quieter and darker areas [13,14]. Although organisms have responded to land-cover

changes and climatic variability throughout history [10], the levels of night lighting and noise now experienced are unprecedented in the evolutionary record. The rapid rise of these novel stimuli could decrease the likelihood that organisms possess the genetic variance to adapt to the altered environmental conditions.

Exposure to anthropogenic noise and artificial light can negatively affect the primary sensory modalities by which most animals interact with their environment. Visual and auditory systems mediate essential behaviors including foraging, predator avoidance, territory defense, and mating decisions [15]. When anthropogenic noise and light disrupt sensory systems we expect a cascade of effects on behaviors and associated life history traits. Light, for example, plays a key role in modulating the circadian rhythms of both invertebrates and vertebrates, and influences longer-term phenological responses [16]. Elevated light at night can reduce fitness through immunosuppression [17] and alter reproductive physiology [18]. In terms of sound stimuli, masking of acoustic cues is a mechanism by

which noise affects animals [11]. This has been studied in the context of songbird communication [12], but masking can also influence perceived risk owing to impaired acoustic surveillance [19]. Other factors, such as distraction of an animal's finite attention [17], have the potential to alter a variety of behaviors and traits.

Mounting evidence suggests that noise and night lighting have strong ecological consequences [2,20], but we know little about how these stimuli can drive evolutionary responses. We argue here that evolutionary responses to these stimuli are highly likely and propose a framework to guide future research (Figure 2), particularly as current studies rarely distinguish between behavioral flexibility (see Glossary), developmental plasticity, or heritable genetic responses. We describe how observed and hypothesized responses to these stimuli by individuals and populations are linked through various mechanisms to evolutionary outcomes. Specifically, we use a reaction-norm approach to show how researchers can investigate light- and sound-derived evolutionary responses. We then discuss how known

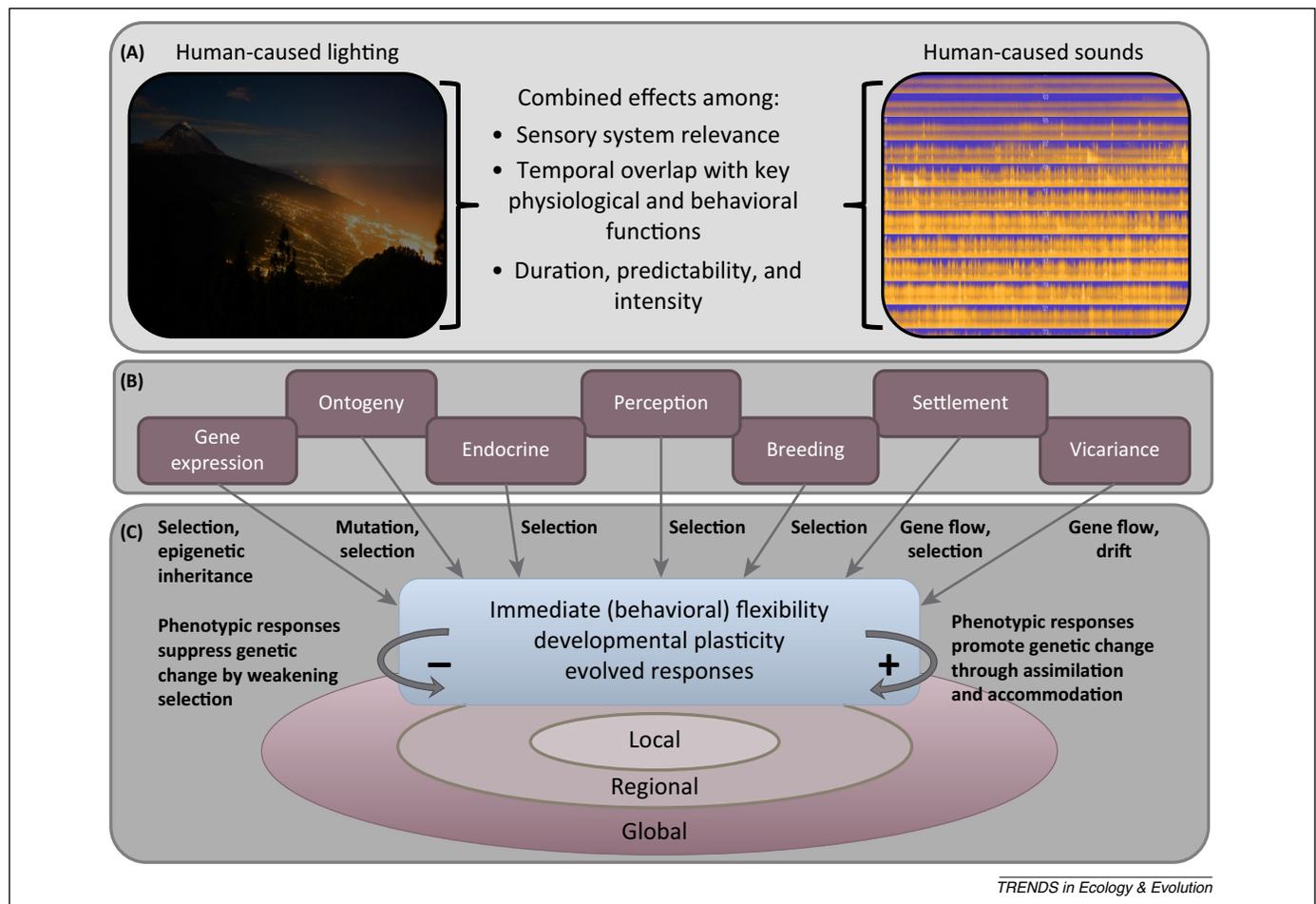


Figure 2. Framework for evaluating how anthropogenic night lighting and sound can influence behavioral, developmental, and evolutionary outcomes. **(A)** Anthropogenic light at night and sound share many features relevant to animal sensory systems. Listed are only a few candidate features of noise and light important to investigating the potential strength of these stimuli as agents of ecological and evolutionary change, whether alone or combined given that these stimuli often co-vary in many environments. See Francis and Barber [11] for a review of some of these features. Because these stimuli can co-occur in many environments, we propose that human alterations of light and sound can act synergistically on wildlife. **(B)** Effects of anthropogenic sound and night at light are known or hypothesized to affect many levels of biological organization, which could result in evolutionary change via different pathways, such as selection, drift, or epigenetic inheritance. Table 1 provides a more comprehensive list of known and hypothesized ecological and evolutionary outcomes due to noise and light. **(C)** Influences of anthropogenic sound and light at different levels of biological organization can result in short-term behavioral flexibility, developmental plasticity, and microevolutionary responses via different evolutionary forces (see Potential Microevolutionary Responses section) and induce responses by individuals and populations over different spatial scales. Importantly, shorter-term phenotypic responses could lead to genetic (evolutionary) change through processes of genetic assimilation and accommodation, which could make evolved responses occur faster or, alternatively, could weaken selection if all genotypes experience high fitness as a result of sound- or light-induced behavioral and developmental shifts.

behavioral and developmental responses could contribute to evolutionary change.

Status of research on anthropogenic light and sound in ecology

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

Anthropogenic sound as a potential selection pressure

Noise can alter physiology, behavior (communication, foraging, vigilance), and population-level metrics such as abundance and density [11]; limited work suggests community-level effects [23]. Most studies have been conducted over short time-periods, and underlying mechanisms are rarely elucidated. Francis and Barber [11] proposed a framework for understanding and predicting behavioral responses and the likely fitness consequences in terms of both acute and chronic noise exposure. Despite these steps towards an understanding of the ecological outcomes of noise, it is unclear to what extent the documented outcomes represent evolutionary changes. Similar to current challenges in understanding tolerance to climate change [10], a central question is whether coping mechanisms among populations that persist in noisy environments reflect behavioral flexibility, developmental plasticity, or microevolutionary responses. Some recent evidence points to short-term behavioral responses [24], but it is unclear whether these might be linked to microevolutionary responses that simply have not received attention (see below).

Anthropogenic light as a potential selection pressure

The crucial role light plays in the regulation of physiology [25] and species interactions [26] has been well studied, but the widespread effects of artificial light received limited research attention until the past decade, starting with Longcore and Rich [27,28]. Until then, most research had focused on documenting large-scale mortality events resulting from the attraction and disorientation of animals (e.g., turtles and birds) by artificial lighting [28]. Research in the past decade, however, has involved numerous biological responses [3,20], including the effects of light on physiology [17], reproduction [29], foraging [30], movement [31], communication [32], and community ecology [33]. In addition to the range of biological responses, studies are now beginning to consider effects from specific light spectra [34]. As with noise pollution, evolutionary implications are largely understudied. One intriguing exception is a study of nocturnal orb-web spiders, which demonstrated that webs were preferentially built in areas that were

artificially lit and, importantly, that the behavior had a heritable basis [35].

From proximate to ultimate effects of anthropogenic light and sound

Organisms respond to anthropogenic light and noise, in a proximate sense, by way of two mechanisms. One mechanism involves immediate adjustments to behavior and physiology, which we define as behavioral flexibility. The other mechanism operates through alterations of developmental processes and gene expression that are influenced by local environmental conditions as the organism develops its phenotype; this is developmental plasticity. Both forms of variation can be visualized as a reaction norm (Figure 3A) which illustrates how phenotypic expression varies across a range of environments. Specifically, developmental plasticity is indicated by the slope of a single reaction norm, and indicates whether a particular genotype varies its ontogenetic production of a phenotype across an environmental gradient. Behavioral flexibility can be visualized as error bars around a particular genotype (Figure 3A). In other words, a genotype (e.g., an individual organism) can vary its behavior within a particular level of the environment, but it can also change its behavior if it experiences a shift in the environment.

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

Adaptive developmental plasticity can increase the strength of selection [38] because genotypes capable of producing the higher fitness phenotypes will be selected for more strongly than those unable to shift ontogeny in this adaptive direction. Even if most genotypes shift in an adaptive direction, mechanisms of genetic accommodation could lead to positive selection [39]. There are few published studies involving developmentally-plastic responses to noise and light relative to evidence for immediate behavioral responses. Recent experiments using mice found early-life exposure to light at night can elevate anxiety behavior in adulthood [40]. This is not surprising given the extent to which photoperiod can impact on the development of mice as a function of altered circadian molecular rhythms during both the perinatal [41] and postnatal phases [42]. In birds, incubation under a long photoperiod results in smaller hatching size, a fitness-related trait [43]. In terms of alteration of the acoustic environment, loud sounds can alter the developmental trajectories of marine invertebrates [44], insects [36], and rodents [45].

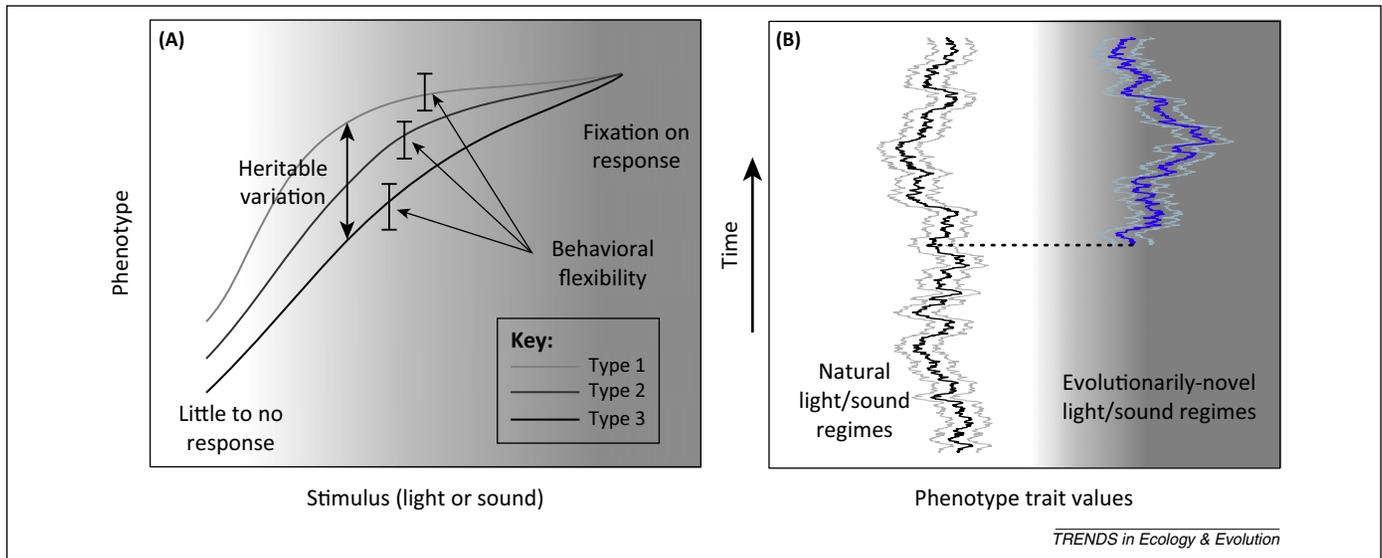


Figure 3. (A) Example reaction norms of phenotypic responses to anthropogenic sound and light. Each line represents the phenotype expressed by a different genotype in the population, across an environmental gradient. The slope of the response represents the developmental plasticity of a genotype. The error bars on each reaction norm represent behavioral flexibility because an individual can alter their phenotype through behavioral mechanisms independently of developmental plasticity. The distance between the lines at any given level of stimulus represents heritable variation, as these are differences in phenotypic expression among the genotypes in the population. (B) Behavioral and developmental responses to anthropogenic sound and light could influence patterns of divergence (modified from Lema [74]). The black line denotes mean phenotypic trait value; grey lines reflect the range of trait variation under natural light and sound regimes. Anthropogenic sound or light could generate rapid phenotypic divergence by triggering behavioral or developmental responses well outside the range of variation in environments without these stimuli (dashed horizontal line). Rapid phenotypic change via developmental or behavioral mechanisms can occur when a population colonizes an environment characterized by novel light and sound regimes, or if these stimuli are rapidly introduced to an existing population. These novel phenotypes (blue line, mean trait value; light blue, range of expression) might then become canalized in the new environment (e.g., genetic assimilation).

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

A central, but relatively unexplored, question is whether the observed variation in a trait responsive to noise or light is best explained by behavioral flexibility or developmental plasticity. If developmental plasticity best explains the variation observed in nature, then it increases opportunities for populations to respond in evolutionary ways. To assess this evolutionary potential, information about the heritability of focal response traits must be collected in the field as the environment is changing (Box 1). Understanding the heritability of traits, and the intensity and direction of selection as they occur in the field, would allow prediction of evolutionary outcomes for populations as well as understanding of current levels of adaptation. Such research must address the complexities of selecting appropriate measurement techniques, equipment, measurement precision, and units for characterization of light and sound environments (Box 2).

Potential microevolutionary responses

Adaptive responses to anthropogenic light and sound require (i) a heritable response in the population (e.g., mating calls), (ii) a mechanism that alters gene frequencies from one generation to the next (e.g., female preference for a specific call frequency), and (iii) evidence that changes in the light and or sound regime are causal agents driving the relationship between heritable response and the

change in gene frequency in the population (e.g., a novel sound changes female preference, which in turn drives changes in call structure). We briefly review additional conditions for evolutionary change with respect to the four most commonly recognized forces of evolution: selection, gene flow, drift, and mutation. These four mechanisms can operate concurrently on the same population in environments influenced by light and noise.

Sensory stimuli as drivers of selection

Artificial light and noise can influence survival [28] and reproduction [32,47] in several animal taxa. Numerous traits are associated with or depend upon the sensory

Box 1. How to measure heritability in the field

To estimate heritability in wild populations we need to disentangle the observed variation in a trait between genetic and environmental components. In addition, within the genetic variance it is often useful to directly estimate the narrow-sense heritability, which tells us how much of variance is due to additive genetic effects (of multiple loci influencing a complex quantitative trait), and is estimated by comparing relatives with each other. In particular, we advocate animal model approaches to estimating heritability [75]. In such a technique, information about the genetic relatedness of individuals in populations is collected to construct pedigrees that are then analyzed using generalized linear model approaches that partition phenotypic variance among possible genetic explanations. One of the advantages of this approach over others is that some statistical models can use incomplete pedigrees that include fairly distant relationships, making the methods relatively amenable to estimating heritability from field population datasets [75]. Many of the traits we propose could evolve in relation to altered anthropogenic light and sound are close to Gaussian-distributed (Table 1), therefore it appears that maximum likelihood approaches to estimating heritability through animal models could be most appropriate in many cases [76].

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

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

Challenges

Range. Both light and sound levels vary over many orders of magnitude, changing on a timescale of seconds to minutes. Sound level is measured on a logarithmic scale, as is light level in astronomy.

Direction of wave propagation. Animal responses usually depend not only on integrated fluxes but also directional information. Glare and contrast can be crucial in artificially lit scenes.

Spectral weighting. Human perception does not necessarily match animal perception, but full spectral measurement is expensive and difficult.

Short-duration variations. Amplitude and frequency modulation might need to be measured for sound; flicker could be important for artificial light.

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

Recommendations

(i) Tradeoffs must be assessed in the planning stage to find a measurement technique that is appropriate to answer the question under investigation. Recording spectral information is highly recommended. Tradeoffs are more acceptable in field experiments, where conditions can be highly variable. Full spectral characterization should be standard in laboratory studies [77]. (ii) Instruments must have sufficient range and precision. Measurements at the edge of the range of an instrument provide insufficient information. (iii) It is likely unnecessary and unproductive to develop mastery in an outside discipline. Find collaborators from outside your field to provide advice and assistance in measurement. As with consulting a statistician, experimental set-up should be discussed with a professional (e.g., a lighting or acoustical engineer).

systems of the animal; thus evolutionary responses to these sensory stimuli will likely carry over to additional life-history traits. For example, both sound and light stimuli alter the configuration of communication systems [15], which could influence other behavioral (e.g., agonistic interactions, mate choice, vigilance, foraging efficiency), morphological (reception and production), and physiological traits (e.g., stress hormone, immune function, metabolism). Substantial evidence indicates that anthropogenic noise and light stimuli elicit phenotypic responses (Table 1). Two traits with moderate heritability and phenotypic change are bird song and circadian rhythms. Bird song in noisy habitats, for example, can display altered structure, timing, amplitude, and frequency parameters [12]. Some components of song production are heritable, such as vocal processing regions of the brain [48] and beak morphology [49]. Interpretation of these observations, however, is complicated by the fact that the syntax and note structure of bird song is learned in most of the species

studied [50], confounding field estimates of heritability. Furthermore, several studies demonstrate that some vocal adjustments in response to noise are likely the result of immediate behavioral flexibility and not adaptive change [24]. It is possible that this behavioral flexibility could still be a leader for evolutionary change (Figure 2C). We posit that bird song remains a likely trait under selection by anthropogenic sensory stimuli, and that the use of cross-fostering experiments in the laboratory paired with field manipulations could prove a powerful approach to unveiling the strength of noise as a selective agent.

Stronger evidence for adaptive change comes from altered light regimes. Circadian rhythms are likely targets of selection because they are ubiquitous in almost all organisms and synchronize to the external environment, with light as the primary Zeitgeber. Although the molecular basis of circadian clocks is highly conserved across taxa [16], heritable variation in circadian rhythms is found within populations [51]. In the great tit (*Parus major*), for example, circadian period length can be highly heritable ($h^2 = 0.86$) and, in relatively closely related blue tits (*Cyanistes caeruleus*), males that sing early have increased annual reproductive output by increasing their extra-pair copulation success [32]. Because both tit species and several other songbirds are known to begin singing earlier in the morning owing to artificial light [32], artificial night lighting might select for earlier chronotypes in birds. Indeed, Dominoni *et al.* [52] demonstrated that European blackbird (*Turdus merula*) urban and rural populations differ in their circadian rhythms and chronotypes, as would be expected from the influence of artificial light. Nevertheless, even in these cases it is difficult to distinguish the sources of variation: how much is due to heritable change and how much to plasticity and flexibility? Traits that are likely under selective pressure from anthropogenic light and sound should be studied using pedigree and animal model studies in the field to directly quantify heritable variation and infer the remaining flexibility and plasticity (Box 1). Crucial experimental manipulations of sound and light stimuli are also necessary to unambiguously identify mechanisms; stimuli that represent relevant changes that populations experience from various forms of human development should be used (Box 3).

Sensory stimuli as drivers of gene flow

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

It is also possible that anthropogenic sensory stimuli create movement barriers and reduce gene flow through

Table 1. Numerous traits are candidates for selection by light at night and anthropogenic noise, and span behavior, morphology, and physiology, some of which are directly related to phenology^a

Trait category	Selective pressure	Candidate traits	Phenotypic change	Heritability estimates ^b		
Communication and behavior	Acoustical environment can mask or interfere with vocal signals, or be timed to interfere with vocal signaling	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 [78]	Not reported		
		Agonistic interactions	Males respond differently to urban songs [12]	Aggression, $h^2 = 0.10$; exploratory behavior, $h^2 = 0.54$ [79]		
		Mate choice	Preference for low-frequency songs erodes with urban noise [72]; noise decreases preference for own mate [80]	Not reported		
		Vigilance	Increased vigilance behavior in noise [81]	Vigilance, $h^2 = 0.08$ [82]		
		Foraging efficiency	Successful foraging bouts decreased, and foraging time increased near noisy roads [83]	Proportion of prey captured in neonates, $h^2 = 0.32-0.54$ [84]		
		Learning and cognition	Reduced learning after noise exposure [55]	Learning in bees, $h^2 = 0.39-0.54$ [85]		
		Sound production	Coupling of amplitude and frequency such that both increase in urban noise [86]	Beak length, depth, and width, $h^2 = 0.65-0.90$ [49]		
	Exposure to light at night around dawn and dusk, and to low light levels at night	Rates and timing of signaling	Increased signaling at times without high noise [87]	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	Advance of reproductive physiology of blackbirds [18]	Not reported		
		Feeding behavior	Increase of chick feeding behavior in great tits [88]	Not reported		
		Nest site choice	Avoidance of light at nest sites by godwits [89]	Not reported		
		Reproduction	Alteration of mating behavior in moths [29]	Not reported		
		Calling and movement behavior	Reduced advertisement call activity, less movement activity [90]	Not reported		
		Emergence time	Delayed emergence time [91]	Not reported		
		Daily timing of feeding behavior	Switch to nocturnal feeding [30]	Not reported		
		Morphology	Acoustical environment can mask or interfere with vocal signals	Sound reception	Individuals respond differently to attenuated versions of vocal signals [92]	Hearing loss, $h^2 = 0.36$ [93]
				Eye size	Reduced eye size	Eye size, $h^2 \leq 0.5$ [94]
Exposure to light at night	Body mass		Reduced mass of juveniles [91]	Not reported		
Physiology	Exposure to increased acoustical noise	Stress hormones	Elevated corticosterone levels [95]	Corticosterone levels, $h^2 \leq 0.27$ [96]		
		Metabolism	Increased oxidative damage in noise [55]	Not reported		
		Cardiovascular health	Increased occurrence of hypertension and cardiovascular disease in humans [97]	Not reported		
	Exposure to low light levels at night	Stress hormones, melatonin	Reduced expression of melatonin, change of pattern of hormone expression [98]	As above		
		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 in blood [17]	Not reported		
		Pheromone release	Suppression of pheromone release	Not reported		

^aThe sample list 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.

^bAbbreviations: h^2 , heritability; HVC, avian brain bird-song nucleus (formerly high vocal center); RA, robust nucleus of the arcopallium.

Box 3. Suitable study systems or potential traits under selection

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

habitat fragmentation. For example, birds that cannot communicate effectively in noisy environments might not traverse this type of matrix. Some mammals tend to avoid artificially lit environments, which would decrease connectivity [31]. A reduction in gene flow could accelerate local adaptation to altered light and sound regimes but could also lead to a loss of genetic variance in the long term.

Sensory stimuli as drivers of genetic drift

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

Sensory stimuli as drivers of mutation

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

In parallel with the noise literature, there is laboratory evidence that light exposure, especially in ultraviolet

wavelengths, increases the probability of genetic mutations, including within the germ lines of several taxa [58]. Thus, the mutagenic potential of anthropogenic ultraviolet light, such as that produced by mercury vapor lamps, represents a further area requiring investigation. While alterations of mutation rates are likely not large enough to affect rapid evolutionary change, we would be remiss to ignore the possible effects of anthropogenic sensory stimuli on direct mutation.

Macroevolutionary patterns

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

Recent divergence and phylogenetic trees

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

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

Differential extinction rates

As celestial signals such as the Milky Way disappear, and night is replaced by extended twilight, species specialized for night-time conditions are likely to be extirpated and species flexible in their behavior with respect to light will benefit [65]. Direct mortality from night lighting can be significant at the population level. For example, fatal attraction to lights has resulted in the extinction of at least two populations of the endangered giant water bug *Lethocerus deyrolli* [66]. In addition, if not offset by rescue efforts, the attraction of young seabirds to urban lights could extirpate Cory’s shearwater *Calonectris diomedea* from the Azores [67]. Well-known declines of nocturnal insects, such as moths [68], have been linked to artificial night lighting, but it is unclear whether this stimuli or other human-induced environmental changes are most responsible. Declines among many taxa might be due to attraction and ‘entrapment’ at lights but, for some taxa,

declines could also reflect interference with sexual signals (e.g., moths [29] or fireflies). Indeed, firefly species richness is lower in areas characterized by 0.2 lux and higher [69].

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

Implications for conservation and biodiversity

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

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

Evolution occurs on a timescale that is at odds with the immediacy of conservation efforts. Stimuli that alter the intensity, duration, and cycles of natural sound and light environments, however, have the potential to drive profound and rapid evolutionary change. Because anthropogenic changes to sound and light are so large relative to natural fluctuations, we propose that human-induced light and sound might be particularly effective agents of selection. Understanding how noise and light might drive selection, as we propose, is a priority for a world that is, unfortunately, increasingly loud and bright.

Acknowledgments

This manuscript was prepared as an outcome of a meeting convened at and funded by the National Evolutionary Synthesis Center (National Science Foundation EF-0905606) to C.B.C., J.R.B., and C.D.F. J.R.B. and

C.D.F. were also supported by National Science Foundation Grant CNH-1414171.

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