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Why conservation biology can benefit from sensory ecology

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Global expansion of human activities is associated with the introduction of novel stimuli, such as anthropogenic noise, artificial lights and chemical agents. Progress in documenting the ecological effects of sensory pollutants is weakened by sparse knowledge of the mechanisms underlying these effects. This severely limits our capacity to devise mitigation measures. Here, we integrate knowledge of animal sensory ecology, physiology and life history to articulate three perceptual mechanisms—masking, distracting and misleading—that clearly explain how and why anthropogenic sensory pollutants impact organisms. We then link these three mechanisms to ecological consequences and discuss their implications for conservation. We argue that this framework can reveal the presence of ‘sensory danger zones’, hotspots of conservation concern where sensory pollutants overlap in space and time with an organism’s activity, and foster development of strategic interventions to mitigate the impact of sensory pollutants. Future research that applies this framework will provide critical insight to preserve the natural sensory world.

Human activities are affecting life on our planet at an unprecedented rate¹. In the last century, there has been tremendous growth in transportation networks, urban land cover and intensive farming². This spectacular level of expansion has heavily relied on technological advancements in engineering, physics and biochemistry¹, but has brought along ecological consequences, such as habitat destruction, biodiversity loss and climate change³. An often overlooked, yet important, consequence of global human expansion is the negative impact on the sensory systems of many organisms, a phenomenon known as sensory pollution⁴. Animals rely on sensory systems (for example, their hearing, vision, smell or electro-perception) to process (a)biotic information on the physical and temporal structure of their environment. The ability to use such environmental information is critical to many ecological processes such as habitat selection, species recognition, foraging efficiency and risk assessment. Human activities interfere with these sensory systems by introducing novel chemical and physical stimuli in the environment. Among known anthropogenic sensory pollutants, acoustic noise, night lighting and chemical agents are globally pervasive, yet still rapidly growing in extent and intensity^{5–9}. These pollutants can fundamentally impact ecological processes by altering how animals process information in their environment^{5,6,10}. Sensory pollution has, therefore, been suggested to have led to

population-level declines of several species, including locally and globally threatened species^{11–14}, and thus poses a substantial threat to the long-term persistence of animal populations and functioning of natural ecosystems.

Ecologists have historically used environmental factors such as vegetation cover, temperature and rainfall to conceptualize and enumerate the conditions necessary for species survival and reproduction, while often ignoring sensory elements of the environment¹⁵. Even when sensory stimuli have been used to quantify species-specific ecological niches, they have been biased by human perception (for example, greenness of vegetation), often failing to account for how different organisms sense the environment¹⁵. For example, bats use ultrasonic frequencies to image their world with sonar¹⁶ and bees use both ultraviolet visual¹⁷ and electromagnetic¹⁸ signals to learn the location of flowers that provide the highest nectar rewards. We argue that by overlooking the sensory world, we are ignoring an entire dimension of species’ niches. As a result, conservation policies and actions are deprived of crucial information about animal–environment relationships across gradients of anthropogenic landscapes. For example, songbird distributions are often defined by vegetation density and type. Yet recent work found that variation in the acoustic environment better explained breeding distributions of two species than did gradients in vegetation¹⁹, emphasizing

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Table 1 | Three different mechanisms describe the impact of sensory pollution across modalities

	Sensory modality	Mechanism	Effect	Reference
Masking	Light pollution	Masking of lunar cues	Desynchronization of coral reef spawning	87
	Noise pollution	Masking of prey cues	Reduced foraging efficiency in bats	29
	Chemical pollution	Masking of sexual signals	Hybridization between two river fish species	32
Distraction	Light pollution	Impact on cognition or memory	Flicker-fusion light impact on chickens	88
	Noise pollution	Reduced attention for predator, prey or mating cues	Reduced anti-predator behaviour in dwarf mongooses	20
	Chemical pollution	Reduced localization of food source	Reduced localization of nectar source by moths	46
Misleading	Light pollution	Misidentification of celestial cues	Attraction of nocturnal insects to artificially lit structures	12
	Noise pollution	Misidentification of predator sounds	Avoidance of naval sonar by cetaceans	53
	Chemical pollution	Misidentification of predator smells	Defence grouping by green algae in response to surfactants	89

Table 1 shows examples of how sensory pollutants across the visual, acoustic and chemical domain can lead to masking, distracting or misleading. For more details on examples, as well as a more extensive list of examples, see Supplementary Table 1.

the benefits of examining existing dogma with a sensory lens. Reimagining conservation to include sensory perspectives conveys pragmatic benefits. Sensory pollutants can be efficiently reduced at their sources, and such reductions offer underutilized opportunities for immediate habitat restoration and improved ecosystem resilience.

Although a growing body of literature demonstrates the widespread impact of anthropogenic sensory pollutants^{4–6,10,20–22}, a considerable theoretical gap still exists regarding the underlying processes by which sensory pollutants influence species' distributions and fitness. Specifically, we lack a framework that explains species' responses to stimuli across sensory systems. Here, we review and synthesize knowledge of animal physiology, life history and sensory ecology, to outline three mechanisms that explain how anthropogenic sensory pollutants alter information processing across organisms and pollutant types. We then describe how these mechanisms link sensory pollutants to a range of ecological consequences. Our ultimate aim is to promote targeted mitigation of sensory pollutants and to guide future sensory ecology research to fill outstanding knowledge gaps.

Impact of sensory pollution on behaviour and physiology

Sensory pollutants can lead to a wide range of behavioural and physiological responses. Behavioural changes have been demonstrated for processes such as migration²³, biological timing^{24,25}, intraspecific communication²⁶, prey detection^{27,28} and predator avoidance²⁹. A very common behavioural response to light pollution is the attraction to light sources. For example, every September, millions of birds migrate south from the temperate regions of the Northern Hemisphere to wintering grounds in Central and South America. For many of these birds, this migration event coincides with New York City's annual 9/11 memorial tribute, consisting of 44 spotlights positioned to form two pillars of high-intensity light pointed skyward. As many bird species use celestial cues to navigate during nocturnal migration, these lights can attract up to 15,000 birds in a single night that will fly in circles inside the beams until morning, often dying from exhaustion and collisions with artificially lit structures²³. Another well-known example is anthropogenic noise produced by traffic and heavy machinery, which is known to impair prey detection or anti-predator behaviour in taxa as diverse as bats, birds and midges^{30,31}. Furthermore, an example of chemical pollution originating from food factories can interfere with mate choice and species recognition in fish³². Some of these examples are listed in Table 1, while a much more extensive list is presented in Supplementary Table 1.

Most observed behavioural responses to sensory pollutants are driven by underlying physiological changes³³. For instance, many organisms show altered activity patterns in response to artificial light at night. Studies in fish and birds have shown that these altered diel behaviours are mediated by changes in the temporal expression of clock genes as well as by altered diel melatonin rhythms^{34–36}. Similarly, the effects of noise on several physiological systems are well documented^{30,37,38}, such as the disruption of glucocorticoid signalling and increased metabolic costs^{37–40}, which have recently been linked to changes in breeding behaviour in birds³⁷. Finally, chemical pesticides can disrupt chemical signalling, such as pheromone production, in many insects⁶, which is likely to be the physiological pathway underlying the effects of chemical pollution on mate choice reported in several insect groups⁶. However, distinguishing between behavioural and physiological impacts may not provide clear insight into the impact of sensory pollutants on animals, as these two processes are tightly interwoven via various feedback systems. Instead, we propose a higher-level distinction between possible impacts of sensory pollution, one that is based on why and how behavioural and physiological responses are produced.

Mechanisms by which sensory pollutants interfere with sensory systems

Sensory pollutants must be first detected by peripheral sensory receptors (for example, the eyes, ears or chemical receptors of animals) and then processed by higher-level cognitive areas (see ref. ⁴ for a general description of the perceptual mechanisms involved in sensory pollution). Importantly, this first detection step depends on the species-specific perceptual sensitivities (for example, some moths are much more sensitive to artificial light that contains energy in the ultraviolet (UV) range). We argue that sensory pollutants can impact behavioural and physiological responses via three main mechanisms. Specifically, sensory pollutants can mask environmental information, distract from the natural processing of information, or introduce erroneous information that misleads animals toward the wrong response. We emphasize that we are not addressing direct physiological effects of high doses of pollutants, which may lead to physical damage, (for example, permanent hearing loss) or chemical intoxication. Rather, we contend that most animals are exposed to low levels of pollutants, which they process through their sensory systems and which have large ecological impacts through our proposed sensory mechanisms.

'Masking' is the process by which the capacity of an organism to detect or discriminate a target stimulus is decreased by the

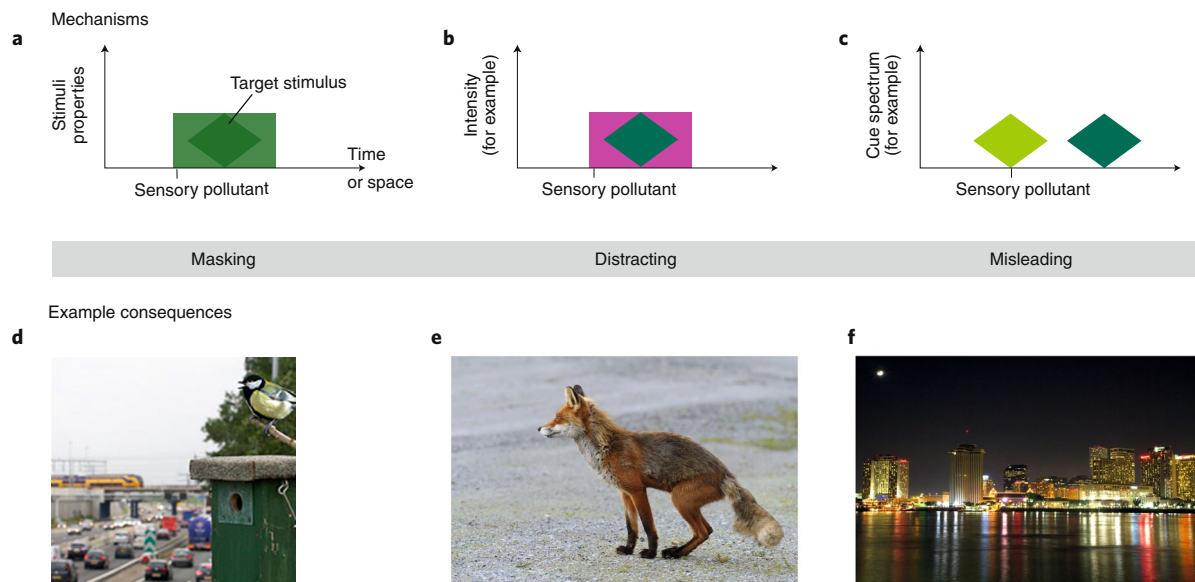


Fig. 1 | Three different mechanisms underlie ecological effects of sensory pollutants. **a–c**, The top row depicts the perceptual processes of masking (**a**), distracting (**b**) and misleading (**c**). The y axes depict either general properties of the signal or cue and the sensory pollutant, or examples of different stimulus dimensions. Masking depends on the overlap in physical properties such as spectrum (for example, hue) and intensity between sensory pollutant and target stimulus (depicted by the similar colours of square and diamond polygon). Distracting does not depend on spectral overlap and can even occur between modalities (for example, the pollutant being a sound and target being a visual cue, hence the different colours for the two polygons). Misleading does not depend on the overlap in time and space between the pollutant and target stimulus (the two polygons do not overlap in time or space, but are similar in shape and colouration). **d–f**, The bottom row depicts example consequences of the different mechanisms. Traffic noise can mask birdsong through spectral–temporal overlap (**d**); sensory pollutants can distract animals, which is particularly important in predator–prey interactions (**e**); artificial light at night can attract migratory birds who mistake high-intensity lights for environmental cues that usually guide their movements (**f**). Credit: Wouter Halfwerk (**d**); blickwinkel / Alamy Stock Photo (**e**); David R. Frazier Photolibrary, Inc. / Alamy Stock Photo (**f**).

interference from a non-target sensory pollutant. By definition, masking occurs within a single sensory modality, when a pollutant is similar in intensity and spectrum to the natural environmental stimulus. That is, the natural stimulus is obscured by the sensory pollutant. For example, masking occurs when the sky glow caused by high levels of artificial light at night impairs detection and discrimination of light from the moon (Fig. 1). Masking affects diverse ecological processes, including the synchronization of tidal rhythms in intertidal organisms⁴¹ or acoustic communication in birds. Another common example of masking is the effect of anthropogenic noise on the detection of acoustic signals and cues. Traffic noise often overlaps in spectral frequency with the songs of several bird species, thereby masking acoustic communication³¹. Chemical pollution can also mask signals and cues, for example, humic acid from industrial wastewater binds to receptors in the olfactory bulb of swordtail fish, blocking the detection of species-specific odours and thereby reducing species recognition³².

‘Distraction’ is the process by which a sensory pollutant interferes with information processing by occupying part of an animal’s finite attentional capacity⁴². In other words, distraction occurs when a sensory pollutant removes all or part of the attention of an animal from the task it is currently performing, even if only temporarily. Distraction does not depend on the overlap in physical properties (for example, light spectrum or sound frequency) between the sensory pollutant and the relevant stimulus; therefore, it can occur within and across sensory modalities (thereby differing from masking). Distracting stimuli can also affect higher-level cognitive processes, such as spatial orientation²⁹ and memory retrieval⁴³. Many examples of distracting stimuli come from studies on humans, showing reduced learning and problem-solving capacity in the presence of high anthropogenic noise levels⁴⁴. Similarly, noise has been found to distract animals during foraging and vigilance for predators^{20,42}.

Light pollution may also distract animals. For instance, flickering laboratory lights can impact the attention of chickens (*Gallus domesticus*)⁴⁵, which is not the case in humans because we perceive these lights as non-flickering. Consequently, without understanding the sensory abilities of chickens, we would not be able to explain the chickens’ response to lighting. Chemical pollution can lead to overstimulation of the olfactory lobe in insects, which may potentially interfere with higher-level processing of chemical signals and cues. For example, moths have decreased ability to locate nectar via flower scents when tested together with novel, structurally dissimilar chemical compounds⁴⁶.

‘Misleading’ is the process by which a sensory pollutant is detected as a natural cue or signal and provokes an inappropriate, and often maladaptive, response (Fig. 1). In other words, the sensory pollutant guides animals in the wrong direction towards the wrong target, often leading to increased mortality via collisions, exhaustion or predation^{47–49}. Because of this, we propose that when misleading sensory cues lead to maladaptive responses they result in ecological traps^{50,51}. A common example of a misleading cue is artificial light at night mimicking celestial cues and thereby attracting animals during dispersal or migration. Anthropogenic noise has also been suggested to act as a misleading cue⁵². For instance, beaked whales might perceive military sonar as killer whale vocalizations, and alter their distributions to avoid the supposed presence of an apex predator⁵³. However, misleading cues might also turn unnatural behaviours into opportunities, by opening new ecological niches that organisms can exploit. For instance, several diurnal bird species are known to increase nocturnal activity when living in areas subjected to light pollution⁵⁴. This behaviour might be adaptive as it can increase fecundity (via more extra-pair mating opportunities⁵⁵) and food intake⁵⁶. However, potential downsides of nocturnal activity in diurnal animals, such as increased predation⁵⁷ or metabolic

disorders associated with disrupted circadian clocks²⁴, are largely overlooked. Chemicals produced by human activities can mislead animals in two different ways, either by altering levels of naturally present compounds, such as organic volatiles that are used by many species to communicate, or by non-specific binding to olfactory receptors⁶. Naturally occurring compounds can be degraded via chemical interaction with anthropogenic compounds, such as NO_x from diesel fumes degrading floral scent compounds and thus leading to reduced attraction of pollinators⁵⁸ (although we do not consider this a case of sensory pollution *sensu stricto*). Human activities can also lead to increased levels of organic volatiles, either produced on purpose, for instance when using pheromone-based insect traps, or as a by-product. Many blood-feeding insects rely on CO₂ to locate their host and can be easily attracted to anthropogenic sources of CO₂ found in industry and traffic⁵⁹.

We contend that these three mechanisms provide substantial inferential power. Below we outline how these mechanisms effectively link animal sensory systems with ecological consequences, including effects on fitness, opening new avenues of research and novel mitigations for conservation.

Linking sensory pollutants to ecological consequences

Sensory pollutants can either directly or indirectly influence an organism's fitness and both pathways can have important population- or community-level consequences. Organisms are directly affected through an impact on their sensory systems (either via masking, distracting or misleading mechanisms) or indirectly affected through changes in the presence and functioning of other species with which they interact. Below we will review these direct versus indirect effects of sensory pollutants in more detail.

Direct fitness consequences of sensory pollution. The behavioural and physiological impacts of light, sound and chemical pollutants mentioned above can translate to reduced survival and reproduction for many organisms, who bear the cost of lost information, reduced processing time and maladaptive decisions. Some of these effects lead to increased mortality, as in the case of misleading birds, insects and turtles to artificial lights^{23,60}. In this situation, the sensory pollutant is effectively creating an ecological trap. Although this can lead to mortalities (that is, entrapment of insects and birds in lights), many effects of sensory pollutants may have less obvious fitness consequences through an impact on health and reproductive output. Indeed, noise generated from road traffic, energy development and military sonar has been related to reduced reproductive success in songbirds and beaked whales^{37,61}. Male newts exposed to low (non-toxic) doses of insecticides demonstrated a delayed response to female odours (that is, masking), which led to a reduction in mating success⁶². Artificial light at night, through circadian disruption, has been shown to affect sleep⁶³ and consequently lead to poor physiological health²⁴.

Examples of direct fitness costs of sensory pollutants are quickly accumulating. Yet, some animals can cope with intense exposure to sensory pollution. For example, individuals can mitigate masking effects by shifting the frequency, intensity or timing of their vocalizations⁶⁴, or by switching to other sensory modalities to detect their prey²⁷. Individuals may also be able to avoid negative effects of distracting stimuli by switching to less difficult tasks to circumvent the costs of divided attention. Perhaps surprisingly, some animals may even benefit from sensory-polluted environments, as these may open novel ecological niches to exploit. For instance, a predator may profit from having the sound of its wingbeats or footsteps masked by loud noise, and although artificial light at night can mislead animals to novel habitats, these might provide safety from predation⁶⁵, expanded foraging time⁶⁶ or increased extra-pair mating opportunities⁶⁵.

Depending on the balance of costs and benefits resulting from sensory pollution, animals may stay in the polluted environment

or leave in the search of a new area with less sensory degradation. In fact, the sensory environment is a fundamental component of habitat selection, influencing an animal's decision about where to settle and whether to stay (see Box 1 for a detailed explanation of this process). For example, pelagic fish⁶⁷ and crab⁶⁸ larvae find their preferred habitat by homing in on the soundscape produced by biotic and abiotic sources in coral reef habitat. Crucially, sensory environments also provide information on habitats to avoid: crustaceans avoid the same reef noise, likely to steer clear of reef predators²⁹. Thus, animals leaving or avoiding sensory-polluted areas might be an important step in a process that eradicates sensitive species and, along with a lack of alternative suitable habitats, ultimately leads to biodiversity decline⁶⁹. For instance, a field experiment using a 'phantom road' has linked traffic noise to a reduction in the occurrence of migrating songbirds at a known stopover site⁷⁰. The decision to stay or leave, to cope or adjust can also affect other species in sensory-polluted areas, which we will review in the next section.

Indirect effects through changes in species interactions. The direct effects of sensory pollutants may cause species to change their behaviour or physiology, thereby affecting their performances, which may ultimately lead to the attraction or avoidance of certain areas. Sensory pollution can thereby indirectly alter important ecological processes, in particular species interactions. For instance, as many species use moonlight to time activity patterns, masking by light pollution can affect the encounter rates of predators and prey animals⁷¹. This might also occur in cases where a species expands its activity into the night as a result of increased visibility due to light pollution. Recent reports have, for example, suggested that peregrine falcons might learn to prey upon songbirds migrating at night over light-polluted areas⁷². Pollination is another example of interaction between species that can be disrupted by sensory pollution. A recent study showed that, in artificially illuminated plant-pollinator communities, nocturnal visits to plants were greatly reduced compared to dark areas. In turn, this resulted in decreased fruiting and impacted not only nocturnal pollinator networks, but also cascaded to diurnal networks²². It is likely that these effects came about because pollinators were misled to artificial light sources, and therefore spent less time visiting flowers.

Indirect effects can even impact processes across trophic levels, as primary producers such as plants may benefit (for example, through reduced herbivory), or suffer (for example, through reduced pollination) from the direct impact of pollutants on primary or secondary consumers. For instance, noise pollution altered the community of animals that prey upon and disperse *Pinus edulis* seeds, potentially explaining reduced seedling recruitment in noisy areas⁷³.

For mitigation measures it is important to distinguish between direct and indirect effects. For example, many bats are attracted to streetlights, likely because of increased insect abundance⁷⁴, and unlikely because of a direct effect of artificial light on bats' sensory systems. In this case, mitigation measures should be targeted to the effect of light on insect attraction.

Population-level consequences. Studies that explicitly link sensory pollutants to population decline are rare. One of the best examples for these population-level effects of sensory pollutants is that of artificial lights and insects¹⁴. Within insects, declines in moth populations in the last few decades have been dramatic, but much more evident for nocturnal than diurnal species, which points to the loss of the night due to light pollution as a likely culprit¹². We contend that understanding the mechanisms altering sensory perception in polluted environments can be considered the first step into developing strategies to mitigate the negative organismal effects of these sensory pollutants, which may also underlie population decline¹². In particular, our conceptual model points to some 'sensory danger zones' in space and time, which are of both ecological and

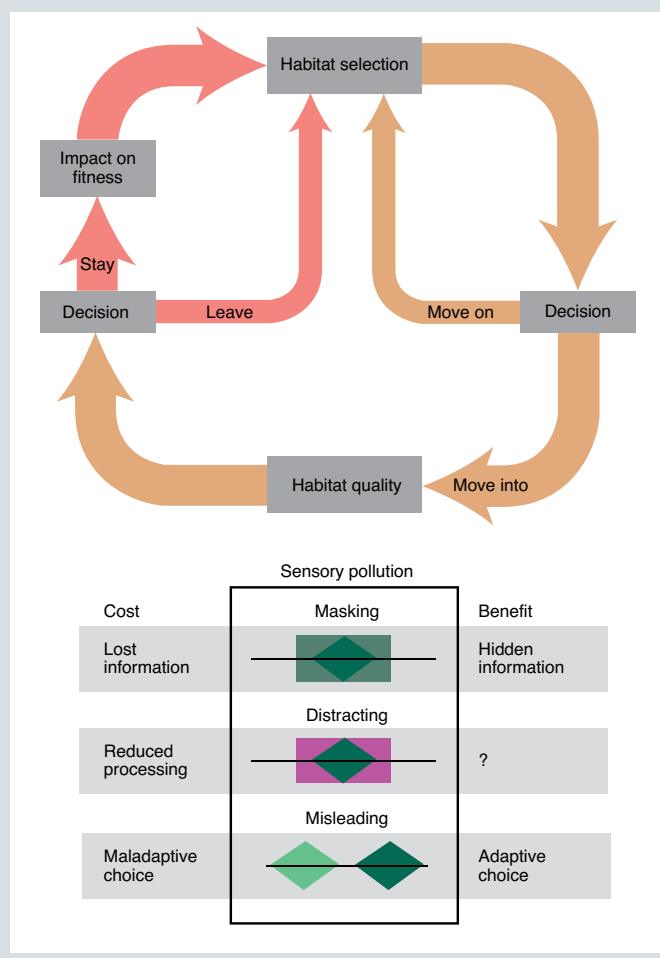
Box 1 | Proposed model of how sensory pollutants may affect habitat quality, habitat choice and ultimately, fitness

Naive organisms initially select habitats ('Habitat selection' box) based on the match between the sensory environment and perceptual sensitivities that have been shaped by evolutionary and developmental processes. Natural sensory cues may be disrupted or corrupted by sensory pollution, which can therefore affect habitat quality and lead to maladaptive habitat selection or avoidance. Sensory pollutants can interfere with decision making ('Decision' box) of initial habitat selection via masking, distracting or misleading, which can cause animals to avoid otherwise suitable habitat ('Move on' arrow) or to settle in suboptimal habitat ('Move into' arrow). For instance, boat noise reduces the attraction of larval fish to playbacks of coral reef sounds, likely via masking²⁰. Yet, boat noise can also act as a misleading cue and increase settlement of vessel hulls, because several invertebrate species appear to mistake engine noise for coral reef soundscapes⁹¹.

Once settled, animals may incur additional costs or benefits associated with sensory-polluted environments, which are going to define the intrinsic habitat quality of a location ('Habitat quality' box). The three different mechanisms come with distinct costs and in some cases distinct benefits, which we summarize in the bottom panel of the figure (see also main-text section 'Linking sensory pollutants to ecological consequences'). In the case of benefits, such as increased foraging opportunities in light-polluted areas, animals may decide to stay (red arrow) and even actively exploit sensory-polluted environments, leading to an increase in fitness ('Impact on fitness' box). In the case of costs, animals may decide to stay and cope via behavioural or physiological adjustments, leading to maintenance of or a reduction in fitness. Alternatively, if the habitat is too degraded by sensory pollutants, animals may decide to leave (red arrow) and search for more favourable habitats.

Previous experience with sensory-polluted environments likely informs future habitat selection and other life-history stages and can thus lead to a cyclic pattern of habitat selection, as shown in the figure. However, for many animals, habitat selection occurs without direct experience in the optimal habitat—instead it is driven by the evolutionary history of selection on innate preferences and the refinement of these preferences via developmental plasticity⁹². For example, naive bats use the echo-acoustic signature of water to select drinking habitat⁹³ and this built-in perceptual bias attracts them to artificial structures with smooth surfaces. Indeed, the bias is so strong that they are even attracted to vertical surfaces, such as large glass windows of office buildings⁹⁴. Polarized light is another hard-wired cue for selecting oviposition sites in myriad aquatic

insects and smooth anthropogenic surfaces such as pavement can mislead these animals to lay their water-adapted eggs where they will soon perish⁹⁵. Understanding the mechanisms underlying animals' selection of sensory environments is an important research frontier. This conceptual model is based on direct effects only for sake of simplicity, although indirect effects, albeit complex, are also crucial to understand⁹⁶. Such indirect effects may often arise through changes in species interactions (see main-text section 'Linking sensory pollutants to ecological consequences').



conservation relevance (Box 2). In the next section, we highlight how adopting a mechanistic sensory lens can reveal potentially different mitigation strategies depending on whether impacts are predominately driven by masking, distracting or misleading effects.

Opportunities for mitigating the effects of sensory pollutants

A mechanistic assessment of animal responses to sensory pollution will facilitate establishing when, where and to which species sensory pollution poses the highest risks. However, it is imperative to consider that not all species are necessarily equally affected by sensory pollution. Organisms are directly affected by sensory pollutants only if such pollutants can be detected by their sensory systems. For example, if the intensity and spectra of the artificial light source does not overlap with the sensitivity of the photoreceptors, an organism is unlikely to be directly affected (but may be indirectly affected, see above). Likewise, anthropogenic noise can only

directly impact organisms when it overlaps with a species' hearing range (other than species that respond to vibrations due to noise)³¹. Thus, we expect that trait-based approaches⁷⁵ that formally combine knowledge of: (1) species' sensory systems; (2) the specific polluting mechanisms that such species may be vulnerable to; and (3) detailed information on exposure from sensory pollutants (such as night light data collected by NASA's satellite-based sensor), will help to formulate specific mitigation measures that better address the underlying causes of the risks (Fig. 2). This could enable forecasting which species might be at higher risk in certain geographic areas and thereby also what geographic areas are hotspots of risk, ultimately serving to prioritize conservation strategies. Below we briefly review how our mechanistic framework may help to design mitigation measures, assuming perceptual or behavioural traits are known for target species or ecosystems.

Species that are at risk of masking pollution will benefit most by reducing the overlap in frequency, wavelength or concentration

Box 2 | Sensory danger zones

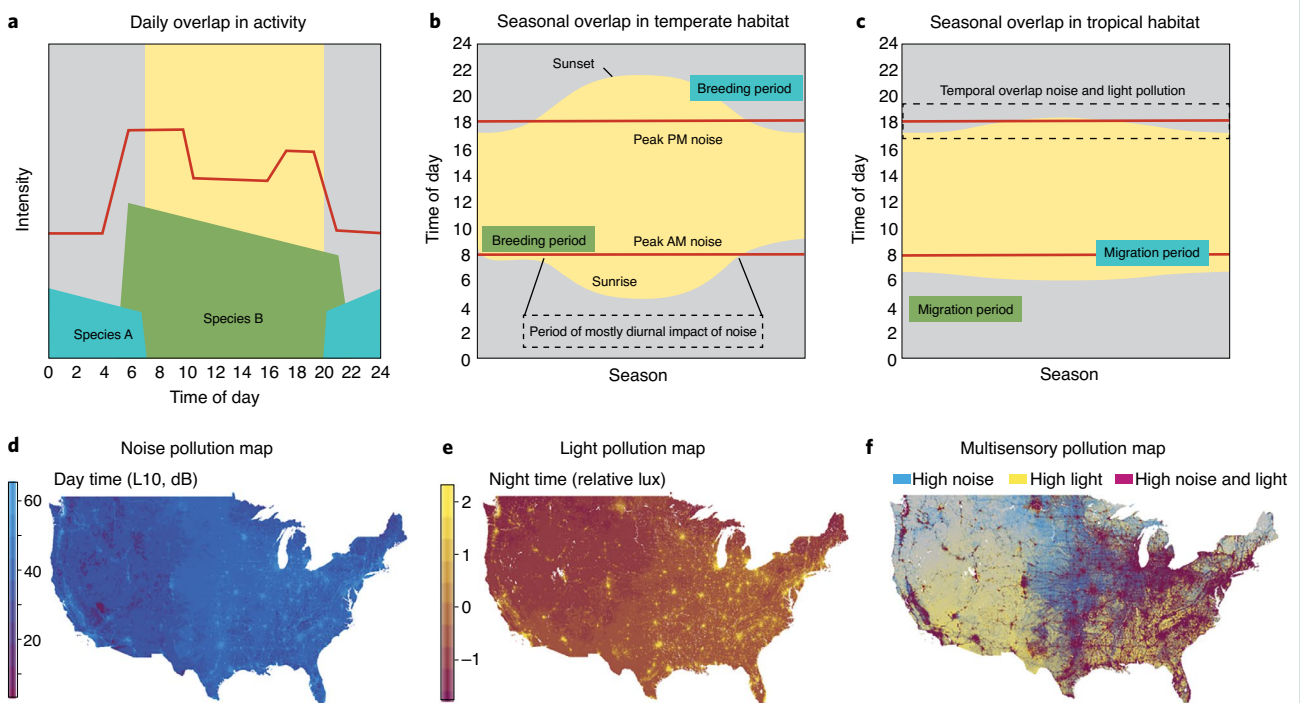
The impact of a sensory pollutant may depend on its spatio-temporal overlap with the distribution and activity of potentially vulnerable species. We thus define 'sensory danger zones' as specific temporal windows or spatial areas in which such overlaps occur. Crucial to this concept is the evidence that sensory pollutants vary in space and time.

We illustrate the concept of sensory danger zones in space and time with two examples: **a**, birdsong and the masking effect of noise; and **b,c**, temporal overlap of noise and light with animal activity at different latitudes. In the first example, songbirds are known to sing predominantly at dawn. In temperate regions, dawn singing occurs mostly in early spring. Depending on the latitude where a species occurs, the peak of dawn song may overlap with the daily peak in traffic noise, the 'rush hour', resulting in noise masking acoustic communication between individual birds⁶¹. In this case the rush hour is the danger zone, but only for birds that live close enough to roads to be subjected to the masking effect of noise⁶¹. However, in our example, such a danger zone disappears during the weekends, when the daily peak in traffic noise occurs later and is not as intense as during the working days. In this case, temporal speed restrictions might alleviate the effects of road noise on nearby ecological communities. For our second example, the peak noise levels during the day never overlap with light at night during the summer at high latitudes, as the days are long, and sunrise and sunset occur much earlier and later than rush hour. In winter, however, there is a strong overlap between light at night and traffic noise, because days are shorter and rush hour can occur before and after sunrise and sunset, respectively. Thus, from a co-exposure perspective, the danger zone is larger in winter than summer (**b**). In tropical regions, such a danger zone might be present throughout the year, because there is little variation in photoperiod in different seasons and peak traffic noise may

occur during dark hours in the presence of light pollution, especially in the evening (**c**).

Sensory pollutant levels also show strong spatial variation. **d–f**, Estimated anthropogenic noise levels (**d**, where L10 is the noise level exceeded for 10% of the time of the measurement duration, in dB), artificial light at night levels (**e**) as well as combined levels of both pollutants (**f**); data from NPS and NASA/NOAA, maps created by N.H.C. Most areas that receive high levels of artificial light at night also receive high levels of anthropogenic noise. However, there is also considerable spatial heterogeneity in exposure to noise, light or both. By taking advantage of existing variation in co-exposure, as well as via experimental manipulations of these stimuli, future research can begin to disentangle the effects of single sensory pollutants as well as to assess their combined effects (additive, synergistic, antagonistic)⁸⁰.

Just as pollutants differ in their spatio-temporal distribution, species likewise differ in their spatial and temporal activity. Indeed, most species can be classified as diurnal, nocturnal or crepuscular. However, many others show considerable flexibility, often depending on external environmental conditions, interspecific relationships or social factors^{97,98}. For instance, a recent meta-analysis highlighted how several mammalian species restrict their activity to night in the face of intense anthropogenic activity, whereas in natural areas the same species may be active during the day⁹⁹. Species also differ in annual activity patterns¹⁰⁰. For instance, some species hibernate, while others are active throughout the winter. Such seasonal changes in the activity of organisms are highly dependent on latitude, or on the environmental gradients that are strongly correlated with latitude. Thus, species will differ in the exposure to sensory pollutants they experience over the course of the day and year, based on their ecology and geographic origin, leading to interspecific variability in sensory danger zones in time and space.



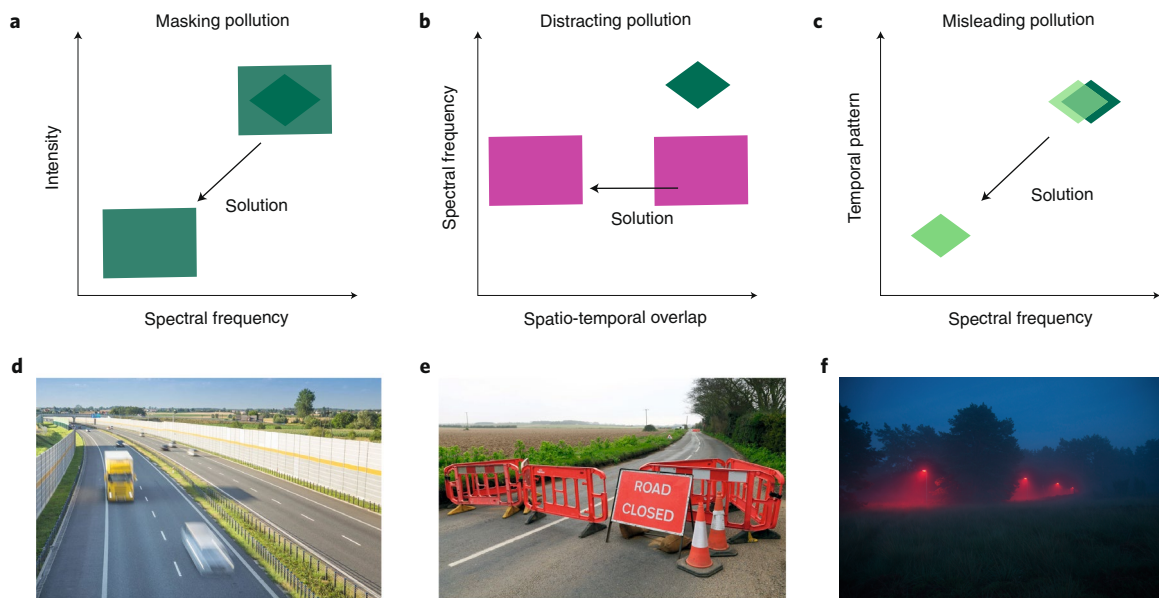


Fig. 2 | Different sensory mechanisms ask for different solutions. Illustrations of the different perceptual problems and associated solutions that may inform cost-effective mitigation measures. Note the different labels to describe the different stimulus dimensions that could be used for mitigation depending on the sensory mechanism. **a**, Masking pollution occurs when the detection or discrimination of a relevant cue is compromised by the overlap in cue parameters with an anthropogenic stimulus. In this example, the natural cue (for example, a birdsong, green diamond) is overlapped in both intensity and spectral frequency with the masking cue (for example, traffic noise, green rectangle). The solution to the problem is to reduce the overlap by either altering the spectral properties, or the intensity of the polluting stimulus. **b**, Distracting pollution occurs when a relevant cue is processed less efficiently due to the presence of a sensory pollutant that takes up some processing capacity by an animal's finite attention. In this example, distracting depends on the overlap in time and space between relevant cue (green diamond) and sensory pollutant (purple rectangle). Reducing the spatio-temporal overlap is likely to be the best solution. Reducing the intensity of the pollutant may also reduce the distracting effect, a feature that is shared with masking pollution. **c**, Misleading pollution occurs when an animal cannot reliably distinguish between a relevant cue (dark-green diamond) and anthropogenic stimulus (light-green diamond). In this example, the cue (for example, lunar light) shares similar spectral and temporal features with the pollutant stimulus (for example, sky glow). The solution is to reduce the similarity in one or more stimulus properties between the cue and misleading pollutant. **d-f**, Examples of mitigation measures associated with the different mechanisms of sensory pollution are depicted in the bottom panels. A sound-attenuating wall can reduce both the intensity as well as frequency content of traffic noise and thereby mitigate both masking and distracting (**d**). Closing of a road during short periods of critical breeding or migration behaviour can reduce spatial-temporal overlap with sensory pollutants, thereby mitigating both masking and distracting (**e**). Shifting the spectrum and timing of artificial light at night can reduce the similarity with cues associated with sunset and sunrise and therefore mitigate misleading pollution (**f**). Credit: yorgil / Alamy Stock Photo (**d**); Holmes Garden Photos / Alamy Stock Photo (**e**); Kamiel Spoelstra (**f**).

(for chemical compounds) between the relevant signal or cue and the polluting stimulus (Fig. 2). For instance, noise abatement such as constructing berms or paving roads with quieter pavement can substantially reduce masking, especially when the spectrum of noise reduced is similar to the relevant stimulus. For example, measures that attenuate noise above 2 kHz may be especially effective at reducing the effect of masking on communication of most songbirds. In the case of light pollution, using light sources of wavelengths outside of the peak photoreceptor sensitivity of most animals will ensure that masking effects are greatly mitigated. For chemical pollution, switching to agents that do not bind to the species-specific receptor cells would reduce masking.

Sensory pollutants that distract animals are perhaps the hardest to mitigate. In these cases, changing spectral or frequency properties of the pollutants will likely have a limited mitigating effect unless the changes move the stimulus outside of the organism's perceptual abilities. When this is not possible, the polluting stimuli must be altered in either the temporal or spatial overlap with relevant (natural) cues or signals. For example, light pollution from headlights that might distract animals near roads could be minimized by designing roadside vegetation and walls to limit the cast of headlights into adjacent habitat, or from temporary road closures, for example during a short, but predictable, peak breeding or migration period. Overpasses with noise- and light-attenuating barriers

could also improve use of such corridors and maintain connectivity by reducing distracting. Mitigation measures to reduce distracting will clearly also benefit masking impacts, but may also be more economically costly, so they could be proposed as a last resort, when masking or misleading mechanisms are unlikely, or their mitigation has proven unsuccessful.

Changing the spectral profile or the temporal pattern of a pollutant may greatly reduce any potential misleading effects. Species that rely on celestial cues for navigation may benefit from the use of artificial lights with specific spectra, such as streetlights that are biased more towards longer wavelengths, which seems to be less disruptive⁷⁶. Importantly, misleading effects may be difficult to mitigate by reducing the intensity of the stimulus, which sets it apart from measures to reduce masking and distracting impacts.

To summarize, in ideal situations solutions to sensory pollution may mitigate two or three mechanisms simultaneously. Indeed, the most straightforward solution is to minimize exposure to pollutants, especially for danger zones (Box 1). However, there will be species-specific problems and settings where focusing on the most outstanding threat relative to the species' sensory system will be the best use of limited conservation resources. In fact, sensory pollutants are unlikely to disappear in the near future: there will be a need for artificial lights, and human activities will probably always emit noise and chemicals in the environment. Our main message is that

there are opportunities for clear conservation strategies based on our proposed sensory mechanisms, which will minimize the impact of sensory pollutants as much as possible.

Conclusions and future directions

The last decade has seen an explosion of studies that have investigated the impacts of light, noise, chemicals and other pollutants on species and ecosystems, but our understanding of the processes that link sensory-pollutant impacts across organisms and modalities has been limited by the lack of frameworks to guide studies and the sheer diversity of sensory capabilities across organisms. We highlight below three outstanding questions that we believe are the most important to advance this field.

1. Is there a direct link between sensory pollutants and population declines? Despite widespread recognition of the impacts of sensory pollutants on organisms' behaviour, physiology and fitness, for much of these effects we still lack clear evidence that they lead to population decline and increased extinction risk. This is a clear research gap that future studies should aim to address, especially for species of conservation concern. Studies that monitor population responses before and after sensory pollutants are introduced in an area, while controlling for population trends in nearby areas without sensory pollutants, would be particularly welcome. Comparative analyses that exploit large-scale, long-term time series of population change and spatio-temporal distribution of pollutants would also be helpful (see Box 1). Moreover, although one of the most obvious outcomes of sensory pollutants is the avoidance of polluted habitats by sensitive species, we do not know what happens to those 'avoiders'. Taken across a large region with considerable sensory pollution and strong avoidance by many species, this likely results in population declines, but more effort is needed to establish such a link.

2. How do different sensory pollutants interact? Although rapidly accumulating evidence demonstrates that sensory pollutants affect behaviour and physiology and consequently fitness, we still understand little as to how such pollutants may interact with each other. Most of these stimuli co-occur in anthropogenic landscapes and waterscapes, and therefore form a complex and relatively novel sensory mosaic that animals must navigate (see also Box 2). Studying each pollutant individually has and will continue to reveal whether a stimulus is responsible for an observed behavioural or physiological response. However, such an approach overlooks the possibility that organisms' responses may change, often in unpredictable and complex ways⁷⁷, when confronted with more than one sensory stimuli. This has profound implications for conservation. If the effect of a pollutant is tested in isolation, but conservation measures are then applied in environments where this pollutant co-occurs with others, these measures may be ineffective or counter-productive. In the worst-case scenario, the mitigation effort might be counter-productive, especially if two pollutants have antagonistic effects.

Thus far, most of the studies on the interactions of different sensory pollutants have been correlational. The combined effects of light and noise on timing of dawn song in birds, for instance, have been assessed in several studies in the field, with conflicting results^{26,54,78,79}. These studies, however, were not specifically designed to experimentally test the interaction between the two stimuli, and thus the interpretation of their outcomes remains challenging. To elucidate the complex interactions that these pollutants may have, robust experimental designs, preferably conducted in the field, are needed. The outcome of such experiments should be assessed using clear guidelines for distinguishing among additive, synergistic or antagonistic effects⁸⁰. A recent experimental field study on host-parasite dynamics used such an approach and was able to reveal an interaction between light and noise intensity on the occurrence of biting midges on *Tungara* frog hosts²¹.

3. What determines species vulnerability to sensory pollutants?

As highlighted above, species vary in the degree to which they perceive and respond to a stimulus. For instance, a comparative analysis on the sensitivity of birds to noise highlighted that species with low-frequency vocalizations were negatively associated with noisy areas, suggesting that the masking effects of noise are likely to exert a strong pressure on habitat selection particularly in those species⁸¹. A trait-based analysis of songbirds has shown that species that possess large eyes relative to body size usually wake up and sing earlier in the morning compared to species with comparatively smaller eyes⁸², which may explain why the latter are less affected by light pollution⁵⁵. In bats, the agile and opportunistic feeding species are abundant around street lights, while slow-flying species avoid these lights, which is likely related to predation risk by owls⁷⁴. Importantly, such effects are wavelength-dependent: green and white light have a strong effect on bat abundance, whereas red light minimizes the effects of light pollution⁷⁴. Similarly, short wavelengths affect moth abundance more than long wavelengths¹², but such effects are mostly found for nocturnal species, while they are absent or limited in diurnal species¹². Dose-dependent impact of sensory pollutants might also be common, as revealed by captive studies of light pollution in birds^{83,84} and fish⁸⁵, as well by field studies on noise pollution and marine mammals⁸⁶. However, such dose-response relationships are not well established for most species affected by sensory pollutants, and this is a critical gap.

The evidence of species-specific responses suggests that a trait-based approach⁷⁵ might enable broad comparisons of key organismal traits that transcend taxa to reveal patterns in community processes and ultimately formulate predictions about impacts of novel environmental pressures such as sensory pollutants. Future useful efforts include: (1) identifying specific traits (that is, sensory, physiological and natural history) that increase susceptibility to sensory pollutants and define their distribution within a population or species; (2) providing a set of predictions that tie specific traits to the underlying sensory mechanisms that we describe in this Perspective (Fig. 1); and (3) projecting the performance of these traits along a gradient of sensory pollutants.

To address these and other questions, future studies should focus on evaluating the benefits of reduced sensory pollution on a wide range of species simultaneously, to identify specific vulnerabilities and the sensory mechanisms that lead to them. Such studies should be as large-scale as possible, to enhance our ability to generalize their results and hence design strategic interventions that will have the highest probability to lead to effective solutions. We anticipate that the next decade of research in this field will bring together mechanism and function to fundamentally advance our understanding of how sensory pollutants impact ecosystems, ultimately ensuring that the best conservation practices will be adopted.

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Author contributions

All authors participated at the workshop in Colorado and actively contributed to round-table discussions. D.M.D., W.H., C.D.F., N.H.C. and J.R.B. laid out the ideas for this manuscript and discussed its content and structure. D.M.D. and W.H. contributed equally to write the initial draft of the paper. C.D.F., N.H.C. and J.R.B. contributed equally to provide feedback and editing on this initial draft. E.B., R.T.B., E.F.-J., K.M.F., M.F.M., D.J.M., E.K.P., B.M.S., D.C.S., J.B.T., C.A.T., L.P.T. and A.W. contributed to this Perspective intellectually and by providing examples and editing. All authors agreed on the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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