Why conservation biology can benefit from sensory ecology

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37

Abstract

39   Global expansion of human activities is associated with the introduction of novel stimuli, such

40   as anthropogenic noise, artificial lights, and chemical agents. Progress in documenting the

41   ecological effects of sensory pollutants is weakened by sparse knowledge of the mechanisms

42   underlying these effects. This severely limits our capacity to devise mitigation measures.

43   Here, we integrate knowledge of animal sensory ecology, physiology, and life history to

44   articulate three perceptual mechanisms – masking, distracting, and misleading – that clearly

45   explain how and why anthropogenic sensory pollutants impact organisms. We then link these

46   three mechanisms to ecological consequences, and discuss their implications for conservation.

47   We argue that this framework can reveal the presence of 'sensory danger zones', hotspots of

48   conservation concern where sensory pollutants overlap in space and time with an organism's

49   activity, and foster development of strategic interventions to mitigate the impact of sensory

50   pollutants. Future research that applies this framework will provide critical insight to preserve

51   the natural sensory world.

52

Main text

Human activities are affecting life on our planet at an unprecedented rate [1]. In the last century there has been tremendous growth in transportation networks, urban land cover and intensive farming [2]. This spectacular level of expansion has relied heavily on technological advancements in engineering, physics and biochemistry [1], but has brought along ecological consequences, such as habitat destruction, biodiversity loss and climate change [3]. 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 pollution [4]. Animals rely on sensory systems (e.g. 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 environment [15]. Even when sensory stimuli have been used to quantify species-specific ecological niches, they have been biased by human perception (e.g., greenness of vegetation), often failing to account for

3

78   how different organisms sense the environment [15]. For example, bats use ultrasonic

79   frequencies to image their world with sonar [16] and bees use both ultraviolet visual [17] and

80   electromagnetic [18] signals to learn the location of flowers that provide the highest nectar

81   rewards. We argue that by overlooking the sensory world, we are ignoring an entire

82   dimension of species' niches. As a result, conservation policies and actions are deprived of

83   crucial information about animal-environment relationships across gradients of anthropogenic

84   landscapes. For example, songbird distributions are often defined by vegetation density and

85   type. Yet recent work found that variation in the acoustic environment better explained

86   breeding distributions of two species than did gradients in vegetation [19], emphasizing the

87   benefits of examining existing dogma with a sensory lens. Reimagining conservation to

88   include sensory perspectives conveys pragmatic benefits. Sensory pollutants can be efficiently

89   reduced at their sources, and such reductions offer underutilized opportunities for immediate

90   habitat restoration and improved ecosystem resilience.

91   Although a growing body of literature demonstrates the widespread impact of

92   anthropogenic sensory pollutants [4–6,10,20–22], a considerable theoretical gap still exists

93   regarding the underlying processes by which sensory pollutants influence species'

94   distributions and fitness. Specifically, we lack a framework that explains species' responses to

95   stimuli across sensory systems. Here, we review and synthesize knowledge of animal

96   physiology, life history and sensory ecology, to outline three mechanisms that explain how

97   anthropogenic sensory pollutants alter information processing across organisms and pollutant

98   types. We then describe how these mechanisms link sensory pollutants to a range of

99   ecological consequences. Our ultimate aim is to promote targeted mitigation of sensory

100   pollutants and to guide future sensory ecology research to fill outstanding knowledge gaps.

101

102   **Impact of sensory pollution on behaviour and physiology**

103   Sensory pollutants can lead to a wide range of behavioural and physiological responses.

104   Behavioural changes have been demonstrated for processes such as migration [23], biological

105   timing [24,25], intraspecific communication [26], prey detection [27,28] and predator avoidance [29]. A

106   very common behavioural response to light pollution is the attraction to light sources. For

107   example, every September, millions of birds migrate south from the temperate regions of the

108   Northern Hemisphere to wintering grounds in Central and South America. For many of these

109   birds, this migration event coincides with New York City's annual 9/11 memorial tribute,

110   consisting of 44 spotlights positioned to form two pillars of high-intensity light pointed

111   skyward. As many bird species use celestial cues to navigate during nocturnal migration,

112   these lights can attract up to 15,000 birds in a single night that will fly in circles inside the

113   beams until morning, often dying from exhaustion and collisions with artificially lit structures

114   [23]. Another well-known example is anthropogenic noise produced by traffic and heavy

115   machinery, which is known to impair prey detection or anti-predator behaviour in taxa as

116   diverse as bats, birds and midges [30,31]. Furthermore, an example of chemical pollution

117   originating from food factories can interfere with mate choice and species recognition in fish

118   [32]. Some of these examples are listed in Table 1, while a much more extensive list is presented

119   in the Supplementary Table 1.

120   Most observed behavioural responses to sensory pollutants are driven by underlying

121   physiological changes [33]. For instance, many organisms show altered activity patterns in

122   response to artificial light at night. Studies in fish and birds have shown that these altered diel

123   behaviours are mediated by changes in the temporal expression of clock genes as well as by

124   altered diel melatonin rhythms [34–36]. Similarly, the effects of noise on several physiological

125   systems are well documented [30,37,38], such as the disruption of glucocorticoid signaling and

126   increased metabolic costs [37–40], which have been recently linked to changes in breeding

127   behaviour in birds [37]. Finally, chemical pesticides can disrupt chemical signaling, such as

128   pheromone production, in many insects [6], which is likely to be the physiological pathway

129   underlying the effects of chemical pollution on mate choice reported in several insect groups

130   [6]. However, distinguishing between behavioural and physiological impacts may not provide

131   clear insight into the impact of sensory pollutants on animals, as these two processes are

132   tightly interwoven via various feedback systems. Instead, we propose a higher-level

133   distinction between possible impacts of sensory pollution, one that is based on *why* and *how*

134   behavioural and physiological responses are produced.

135

Mechanisms by which sensory pollutants interfere with sensory systems

137   Sensory pollutants must be first detected by peripheral sensory receptors (e.g. the eyes, ears or

138   chemical receptors of animals) and then processed by higher-level cognitive areas (see [4] for a

139   general description of the perceptual mechanisms involved in sensory pollution). Importantly,

140   this first detection step depends on the species-specific perceptual sensitivities (e.g. some

141   moths are much more sensitive to artificial light that contains energy in the UV range). We

142   argue that sensory pollutants can impact behavioural and physiological responses via three

143   main mechanisms. Specifically, sensory pollutants can mask environmental information,

144   distract from the natural processing of information, or introduce erroneous information that

145   misleads animals toward the wrong response. We emphasize that we are not addressing direct

146   physiological effects of high doses of pollutants, which may lead to physical damage, (e.g.

147   permanent hearing loss) or chemical intoxication. Rather, we contend that most animals are

148   exposed to low levels of pollutants, which they process through their sensory systems and

149   which have large ecological impacts through our proposed sensory mechanisms.

150

151   *Masking* is the process by which the capacity of an organism to detect or discriminate a target

152   stimulus is decreased by the interference from a non-target sensory pollutant. By definition,

153 masking occurs within a single sensory modality, when a pollutant is similar in intensity and

154 spectrum to the natural environmental stimulus. That is, the natural stimulus is obscured by

155 the sensory pollutant. For example, masking occurs when the sky glow caused by high levels

156 of artificial light at night impairs detection and discrimination of light from the moon (Fig. 1).

157 Masking affects diverse ecological processes, including the synchronization of tidal rhythms

158 in intertidal organisms [41] or acoustic communication in birds . Another common example of

159 masking is the effect of anthropogenic noise on the detection of acoustic signals and cues.

160 Traffic noise often overlaps in spectral frequency with the songs of several bird species,

161 thereby masking acoustic communication [31]. Chemical pollution can also mask signals and

162 cues, for example, humic acid from industrial waste water binds to receptors in the olfactory

163 bulb of swordtail fish, blocking the detection of species-specific odours and thereby reducing

164 species recognition [32].

165

166 *Distraction* is the process by which a sensory pollutant interferes with information processing

167 by occupying part of an animal's finite attentional capacity [42]. In other words, distraction

168 occurs when a sensory pollutant removes all or part of the attention of an animal from the task

169 it is currently performing, even if only temporarily. Distraction does not depend on the

170 overlap in physical properties (e.g. light spectrum or sound frequency) between the sensory

171 pollutant and the relevant stimulus; therefore, it can occur within and across sensory

172 modalities (thereby differing from masking). Distracting stimuli can also affect higher-level

173 cognitive processes, such as spatial orientation [29] and memory retrieval [43]. Many examples of

174 distracting stimuli come from studies on humans, showing reduced learning and problem-

175 solving capacity in the presence of high anthropogenic noise levels [44]. Similarly, noise has

176 been found to distract animals during foraging and vigilance for predators [20,42]. Light

177 pollution may also distract animals. For instance, flickering laboratory lights can impact

178 chickens' (*G. domesticus*) attention [45], which is not the case in humans because we perceive

179 these lights as non-flickering. Consequently, without understanding the sensory abilities of

180 chickens, we would not be able to explain the chickens' response to lighting. Chemical

181 pollution can lead to overstimulation of olfactory lobe in insects, which may potentially

182 interfere with higher level processing of chemical signals and cues. For example, moths have

183 decreased ability to locate nectar via flower scents when tested together with a novel,

184 structurally dissimilar chemical compounds [46].

185

186 *Misleading* is the process by which a sensory pollutant is detected as a natural cue or signal

187 and provokes an inappropriate, and often maladaptive, response (Fig. 1). In other words, the

188 sensory pollutant guides animals in the wrong direction towards the wrong target, often

189 leading to increased mortality via collisions, exhaustion or predation [47–49]. Because of this, we

190 propose that when misleading sensory cues lead to maladaptive responses they result in

191 ecological traps [50,51]. A common example of a misleading cue is artificial light at night

192 mimicking celestial cues and thereby attracting animals during dispersal or migration.

193 Anthropogenic noise has also been suggested to act as a misleading cue [52]. For instance,

194 beaked whales might perceive military sonar as killer whale vocalizations, and alter their

195 distributions to avoid the supposed presence of an apex predator [53]. However, misleading cues

196 might also turn unnatural behaviours into opportunities, by opening new ecological niches

197 that organisms can exploit. For instance, several diurnal bird species are known to increase

198 nocturnal activity when living in areas subjected to light pollution [54]. This behaviour might be

199 adaptive as it can increase fecundity (via more extra-pair mating opportunities[55]) and food

200 intake [56]. However, potential downsides of nocturnal activity in diurnal animals, such as

201 increased predation [57] or metabolic disorders associated with disrupted circadian clocks [24], are

202 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 receptors [6]. 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 pollinators [58] (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 CO_2 to

locate their host and can be easily attracted to anthropogenic sources of CO_2 found in industry

and traffic [59].

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

228 The behavioural and physiological impacts of light, sound, and chemical pollutants mentioned

229 above can translate to reduced survival and reproduction for many organisms, who bear the

230 cost of lost information, reduced processing time and maladaptive decisions. Some of these

231 effects lead to increased mortality, as in the case of misleading birds, insects and turtles to

232 artificial lights [23,60]. In this situation, the sensory pollutant is effectively creating an ecological

233 trap. Although this can lead to mortalities (i.e., entrapment of insects and birds in lights),

234 many effects of sensory pollutants may have less obvious fitness consequences through an

235 impact on health and reproductive output. Indeed, noise generated from road traffic, energy

236 development, and military sonar has been related to reduced reproductive success in songbirds

237 and beaked whales [37,61]. Male newts exposed to low (non-toxic) doses of insecticides

238 demonstrated a delayed response to female odors (i.e., masking), which led to a reduction in

239 mating success [62]. Artificial light at night, through circadian disruption, has been shown to

240 affect sleep [63] and consequently lead to poor physiological health [24].

241   Examples of direct fitness costs of sensory pollutants are quickly accumulating. Yet,

242 some animals can cope with intense exposure to sensory pollution. For example, individuals

243 can mitigate masking effects by shifting the frequency, intensity or timing of their

244 vocalizations [64], or by switching to other sensory modalities to detect their prey [27]. Individuals

245 may also be able to avoid negative effects of distracting stimuli by switching to less difficult

246 tasks to circumvent the costs of divided attention. Perhaps surprisingly, some animals may

247 even benefit from sensory polluted environments, as these may open novel ecological niches

248 to exploit. For instance, a predator may profit from having the sound of its wingbeats or

249 footsteps masked by loud noise, and although artificial light at night can mislead animals to

250 novel habitats, these might provide safety from predation [65], expanded foraging time [66] or

251 increased extra-pair mating opportunities [55].

252   Depending on the balance of costs and benefits resulting from sensory pollution,

253   animals may stay in the polluted environment or leave in the search of a new area with less

254   sensory degradation. In fact, the sensory environment is a fundamental component of habitat

255   selection, influencing an animal's decision about where to settle and whether to stay (see Box

256   1 for a detail explanation of this process). For example, pelagic fish [67] and crab [68] larvae find

257   their preferred habitat by homing in on the soundscape produced by biotic and abiotic sources

258   in coral reef habitat. Crucially, sensory environments also provide information on habitats to

259   avoid: crustaceans avoid the same reef noise, likely to steer clear of reef predators [29]. Thus,

260   animals leaving or avoiding sensory-polluted areas might be an important step in a process

261   that eradicates sensitive species and, along with a lack of alternative suitable habitats,

262   ultimately leads to biodiversity decline [69]. For instance, a field experiment using a "phantom

263   road" has linked traffic noise to a reduction in the occurrence of migrating songbirds at a

264   known stopover site [70]. The decision to stay or leave, to cope or adjust can also affect other

265   species in sensory polluted areas, which we will review in the next section.

266

267   *Indirect effects through changes in species interactions*

268   The direct effects of sensory pollutants may cause species to change their behavior or

269   physiology, thereby affecting their performances, which may ultimately lead to the attraction

270   or avoidance of certain areas. Sensory pollution can thereby indirectly alter important

271   ecological processes, in particular species interactions. For instance, as many species use

272   moonlight to time activity patterns, masking by light pollution can affect the encounter rates

273   of predators and prey animals [71]. This might also occur in cases where a species expands its

274   activity into the night as a result of increased visibility due to light pollution. Recent reports

275   have for example suggested that peregrine falcons might learn to prey upon songbirds

276   migrating at night over light-polluted areas [72]. Pollination is another example of interaction

277   between species that can be disrupted by sensory pollution. A recent study showed that, in

278   artificially illuminated plant–pollinator communities, nocturnal visits to plants were greatly

279   reduced compared to dark areas. In turn, this resulted in decreased fruiting and impacted not

280   only nocturnal pollinator networks, but also cascaded to diurnal networks [22]. It is likely that

281   these effects came about because pollinators were misled to artificial light sources, and

282   therefore spent less time visiting flowers.

283   Indirect effects can even impact processes across trophic levels, as primary producers such as

284   plants may benefit (e.g., reduced herbivory), or suffer (e.g., reduced pollination) from the

285   direct impact of pollutants on primary or secondary consumers. For instance, noise pollution

286   altered the community of animals that prey upon and disperse *Pinus edulis* seeds, potentially

287   explaining reduced seedling recruitment in noisy areas [73].

288   For mitigation measures it is important to distinguish between direct and indirect effects. For

289   example, many bats are attracted to streetlights, likely because of increased insect abundance

290   [74], and unlikely because of a direct effect of artificial light on bats' sensory systems.

291   Mitigation measures should in this case be targeted to the effect of light on insect attraction.

292

293   *Population-level consequences*

294   Studies that explicitly link sensory pollutants to population decline are rare. One of the best

295   examples for these population-level effects of sensory pollutants is that of artificial lights and

296   insects [14]. Within insects, declines in moth populations in the last few decades have been

297   dramatic, but much more evident for nocturnal than diurnal species, which points to the loss

298   of the night due to light pollution as a likely culprit [12]. We contend that understanding the

299   mechanisms altering sensory perception in polluted environments can be considered the first

300   step into developing strategies to mitigate the negative organismal effects of these sensory

301   pollutants, which may also underlie population decline [12]. In particular, our conceptual model

302 points to some 'sensory danger zones' in space and time, which are of both ecological and

303 conservation relevance (Box 2). In the next section, we highlight how adopting a mechanistic

304 sensory lens can reveal potentially different mitigation strategies depending on whether

305 impacts are predominately driven by masking, distracting or misleading effects.

306

Solution to pollution: Opportunities for mitigating the effects of sensory pollutants

309 A mechanistic assessment of animal responses to sensory pollution will facilitate establishing

310 when, where and to which species sensory pollution poses the highest risks. However, it is

311 imperative to consider that not all species are necessarily equally affected by sensory

312 pollution. Organisms are directly affected by sensory pollutants only if such pollutants can be

313 detected by their sensory systems. For example, if the intensity and spectra of the artificial

314 light source does not overlap with the sensitivity of the photoreceptors, an organism is

315 unlikely to be directly affected (but may indirectly so, see above). Likewise, anthropogenic

316 noise can only directly impact organisms when it overlaps with a species' hearing range

317 (other than species that respond to vibrations due to noise)[31]. Thus, we expect that trait-based

318 approaches [75] that formally combine knowledge of (i) species sensory systems, (ii) the

319 specific polluting mechanisms that such species may be vulnerable to, and (iii) detailed

320 information on exposure from sensory pollutants (such as night light data collected by

321 NASA's satellite-based sensor), will help to formulate specific mitigation measures that better

322 address the underlying causes of the risks (Fig. 2). This could enable forecasting which

323 species might be at higher risk in certain geographic areas and thereby also what geographic

324 areas are hotspots of risk, ultimately serving to prioritize conservation strategies. Below we

325 briefly review how our mechanistic framework may help to design mitigation measures,

326 assuming perceptual or behavioural traits are known for target species or ecosystems.

13

327   Species that are at risk of masking pollution will benefit most by reducing the overlap

328   in frequency, wavelength or concentration (for chemical compounds) between the relevant

329   signal or cue and the polluting stimulus (Fig. 2). For instance, noise abatement such as

330   constructing berms or paving roads with quieter pavement can substantially reduce masking,

331   especially when the spectrum of noise reduced is similar to the relevant stimulus. For

332   example, measures that attenuate noise above 2 kHz may be especially effective at reducing

333   the effect of masking on communication of most songbirds. In the case of light pollution,

334   using light sources of wavelengths outside of the peak photoreceptor sensitivity of most

335   animals will ensure that masking effects are greatly mitigated. For chemical pollution,

336   switching to agents that do not bind to the species-specific receptor cells would reduce

337   masking.

338   Sensory pollutants that distract animals are perhaps the hardest to mitigate. In these

339   cases, changing spectral or frequency properties of the pollutants will likely have a limited

340   mitigating effect unless the changes move the stimulus outside of the organism's perceptual

341   abilities. When this is not possible, the polluting stimuli must be altered in either the temporal

342   or spatial overlap with relevant (natural) cues or signals. For example, light pollution from

343   headlights that might distract animals near roads could be minimized by designing roadside

344   vegetation and walls to limit the cast of headlights into adjacent habitat, or from temporary

345   road closures, for example during a short, but predictable, peak breeding or, migration period.

346   Overpasses with noise and light attenuating barriers could also improve use of such corridors

347   and maintain connectivity by reducing distracting. Mitigation measures to reduce distracting

348   will clearly also benefit masking impacts, but may also be more economically costly, so they

349   could be proposed as a last resort, when masking or misleading mechanisms are unlikely, or

350   their mitigation has proven unsuccessful.

351   Changing the spectral profile or the temporal pattern of a pollutant may greatly reduce

352 any potential misleading effects. Species that rely on celestial cues for navigation may benefit

353 from the use of artificial lights with specific spectra, such as streetlights that are biased more

354 towards longer wavelengths, which seems to be less disruptive [76]. Importantly, misleading

355 effects may be difficult to mitigate by reducing the intensity of the stimulus, which sets it

356 apart from measures to reduce masking and distracting impacts.

357   To summarise, in ideal situations solutions to sensory pollution may mitigate two or

358 three mechanisms simultaneously. Indeed, the most straightforward solution is to minimize

359 exposure to pollutants, especially for danger zones (Box 1). However, there will be species-

360 specific problems and settings where focusing on the most outstanding threat relative to the

361 species' sensory system will be the best use of limited conservation resources. In fact, sensory

362 pollutants are unlikely to disappear in the near future: there will be a need for artificial lights,

363 and human activities will probably always emit noise and chemicals in the environment. Our

364 main message is that there are opportunities for clear conservation strategies based on our

365 proposed sensory mechanisms, which will minimize the impact of sensory pollutants as much

366 as possible.

367

Conclusions and future directions

369 The last decade has seen an explosion of studies that have investigated the impacts of light,

370 noise, chemicals and other pollutants on species and ecosystems, but our understanding of the

371 processes that link sensory pollutant impacts across organisms and modalities has been

372 limited by the lack of frameworks to guide studies and the sheer diversity of sensory

373 capabilities across organisms. We highlight below three outstanding questions that we believe

374 are the most important to advance this field.

375

376   *1) Is there a direct link between sensory pollutants and population declines?*

377   Despite widespread recognition of the impacts of sensory pollutants on organisms' behaviour,

378   physiology and fitness, for much of these effects we still lack clear evidence that they lead to

379   population decline and increased extinction risk. This is a clear research gap that future

380   studies should aim to address, especially for species of conservation concern. Studies that

381   monitor population responses before and after sensory pollutants are introduced in an area,

382   while controlling for population trends in nearby areas without sensory pollutants, would be

383   particularly welcome. Comparative analyses that exploit large-scale, long-term time series of

384   population change and spatio-temporal distribution of pollutants would also be helpful (see

385   Box 1). Moreover, although one of the most obvious outcomes of sensory pollutants is the

386   avoidance of polluted habitats by sensitive species, we do not know what happens to those

387   "avoiders". Taken across a large region with considerable sensory pollution and strong

388   avoidance by many species, this likely results in population declines, but more effort is

389   needed to establish such a link.

390

391   *2) How do different sensory pollutants interact?*

392   Although rapidly accumulating evidence demonstrates that sensory pollutants affect

393   behaviour and physiology and consequently fitness, we still understand little as to how such

394   pollutants may interact with each other. Most of these stimuli co-occur in anthropogenic

395   landscapes and waterscapes, and therefore form a complex and relatively novel sensory

396   mosaic that animals must navigate (see also Box 2). Studying each pollutant individually has

397   and will continue to reveal whether a stimulus is responsible for an observed behavioural or

398   physiological response. However, such an approach overlooks the possibility that organisms'

399   responses may change, often in unpredictable and complex ways [77], when confronted with

400   more than one sensory stimuli. This has profound implications for conservation. If the effect

401   of a pollutant is tested in isolation, but conservation measures are then applied in

402   environments where this pollutant co-occurs with others, these measures may be ineffective or

403   counter-productive. In the worst-case scenario, the mitigation effort might be counter-

404   productive, especially if two pollutants have antagonistic effects.

405   Thus far, most of the studies on the interactions of different sensory pollutants have been

406   correlational. The combined effects of light and noise on timing of dawn song in birds, for

407   instance, have been assessed in several studies in the field, with conflicting results [26,54,78,79].

408   These studies, however, were not specifically designed to experimentally test the interaction

409   between the two stimuli, and thus the interpretation of their outcomes remains challenging. To

410   elucidate the complex interactions that these pollutants may have, robust experimental

411   designs, preferably conducted in the field, are needed. The outcome of such experiments

412   should be assessed using clear guidelines for distinguishing among additive, synergistic or

413   antagonistic effects [80]. A recent experimental field study on host-parasite dynamics used such

414   an approach and was able to reveal an interaction between light and noise intensity on the

415   occurrence of biting midges on Tungara frog hosts [21].

416

417   *3) What determines species vulnerability to sensory pollutants?*

418   As highlighted above, species vary in the degree to which they perceive and respond to a

419   stimulus. For instance, a comparative analysis on the sensitivity of birds to noise highlighted

420   that species with low-frequency vocalizations were negatively associated with noisy areas,

421   suggesting that the masking effects of noise are likely to exert a strong pressure on habitat

422   selection particularly in those species [81]. A trait-based analysis of songbirds has shown that

423   species that possess large eyes relative to body size usually wake up and sing earlier in the

424   morning compared to species with comparatively smaller eyes [82], which may explain why the

425   latter are less affected by light pollution [55]. In bats, the agile and opportunistic feeding species

426   are abundant around street lights, while slow-flying species avoid these lights, which is likely

427   related to predation risk by owls [74]. Importantly, such effects are wavelength-dependent:

428   green and white light have a strong effect on bat abundance, whereas red light minimizes the

429   effects of light pollution [74]. Similarly, short-wavelengths affect moth abundance more than

430   long-wavelengths [12], but such effects are mostly found for nocturnal species, while they are

431   absent or limited in diurnal species [12]. Dose-dependent impact of sensory pollutants might

432   also be common, as revealed by captive studies of light pollution in birds [83,84] and fish [85], as

433   well by field studies on noise pollution and marine mammals [86]. However, such dose-response

434   relationships are not well established for most species affected by sensory pollutants, and this

435   is a critical gap.

436   The evidence of species-specific responses suggests that a trait-based approach [75]

437   might enable broad comparisons of key organismal traits that transcend taxa to reveal patterns

438   in community processes and ultimately formulate predictions about impacts of novel

439   environmental pressures such as sensory pollutants. Future useful efforts include *i)* identifying

440   specific traits (i.e. sensory, physiological, and natural history) that increase susceptibility to

441   sensory pollutants and define their distribution within a population or species, *ii)* providing a

442   set of predictions that tie specific traits to the underlying sensory mechanisms that we

443   describe in this paper (Fig. 1), and *iii)* projecting the performance of these traits along a

444   gradient of sensory pollutants.

445

446   To address these and other questions, future studies should focus on evaluating the benefits of

447   reduced sensory pollution on a wide range of species simultaneously, to identify specific

448   vulnerabilities and the sensory mechanisms that lead to them. Such studies should be as large-

449   scale as possible, to enhance our ability to generalize their results and hence design strategic

450   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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Authors contributions

All authors participated at the workshop in Colorado and actively contributed to round-table discussions. DMD, WH, CDF, NHC and JRB laid out the ideas for this manuscript and discussed its content and structure. DMD and WH contributed equally to write the initial draft of the paper. CDF, NHC and JRB contributed equally to provide feedback and editing on this initial draft. EB, RTB, EFJ, KMF, MFMcK, DJM, EKP, LPT, BMS, DCS, JBT, CAT, LPT, AW contributed to this paper intellectually and by providing examples and editing. All authors agreed on the final version of the manuscript.

Competing interests

We declare no competing interests.

Figure legends

Figure 1. The three different mechanisms underlie ecological effects of sensory pollutants. 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 (e.g., hue) and intensity between sensory pollutant and target stimulus (depicted by square and diamond polygon having similar colors). Distracting does not depend on spectral overlap and can even occur between modalities (e.g., pollutant being a sound and target being a visual cue, hence the different colors for the two polygons). Misleading does not depend on the overlap in time and space between pollutant and target stimulus (the two polygons do not overlap in time or space, but are similar in shape and coloration). Bottom-row depicts example consequences of the different mechanisms. Traffic noise can mask bird song 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).

Figure 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. Masking pollution occurs when the detection or discrimination of a relevant cue is compromised by the overlap in cue parameters with an anthropogenic stimulus (a). In this example, the natural cue (e.g. a birdsong, green diamond) is overlapped in both intensity and spectral frequency with the masking cue (e.g. traffic noise, green square). The solution to the problem is to reduce the overlap by either altering the spectral properties, or the intensity of the polluting stimulus. 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 (b). In this example, distracting depends on the overlap in time and space between relevant cue (green diamond) and sensory pollutant (purple square). 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. <u>Misleading pollution</u> occurs when an animal cannot reliably distinguish between a relevant cue (green diamond) and anthropogenic stimulus (light-green diamond) (c). In this example, the cue (e.g. lunar light) shares similar spectral and temporal features with the pollutant stimulus (e.g. skyglow). The solution is to reduce the similarity in one or more stimulus properties between the cue and misleading pollutant. 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 €. 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).

Table 1. Three different mechanisms describe the impact of sensory pollution across modalities. Here we provide 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. References: 1. [87], 2.[29], 3. [32], 4. [88], 5. [20]; 6. [46], 7. [12]; 8. [53]; 9. [89].

	Sensory modality	Mechanism	Effect	Ref.
MASKING	Light pollution	Masking of lunar cues	Desynchronization of coral reef spawning	[1]
	Noise pollution	Masking of prey cues	Reduced foraging efficiency in bats	[2]
	Chemical pollution	Masking of sexual signals	Hybridization between two river fish species	[3]
DISTRACTION	Light pollution	Impact on cognition/memory	Flicker-fusion light impact on chickens	[4]
	Noise pollution	Reduced attention for predator, prey or mating cues	Reduced anti-predator behaviour in dwarf mongooses	[5]
	Chemical pollution	Reduced localization of food source	Reduced localization of nectar source by moths	[6]
MISLEADING	Light pollution	Misidentification of celestial cues	Attraction of nocturnal insects to artificially lit structures	[7]
	Noise pollution	Misidentification of predator sounds	Avoidance of naval sonar by cetaceans	[8]
	Chemical pollution	Misidentification of predator smells	Defence grouping by green algae in response to surfactants	[9]

Box legends

804

805 **Box 1.** Proposed model of how sensory pollutants may affect habitat quality, habitat choice

806 and ultimately, fitness. Naïve organisms initially select habitats (HABITAT SELECTION

807 box) based on the match between the sensory environment and perceptual sensitivities that

808 have been shaped by evolutionary and developmental processes. Natural sensory cues may be

809 disrupted or corrupted by sensory pollution, which can therefore affect habitat quality and

810 lead to maladaptive habitat selection or avoidance. Sensory pollutants can interfere with

811 decision making (DECISION box) of initial habitat selection via masking, distracting or

812 misleading, which can cause animals to avoid otherwise suitable habitat (MOVE ON box) or

813 to settle in suboptimal habitat (MOVE INTO box). For instance, boat noise reduces the

814 attraction of larval fish to playbacks of coral reef sounds, likely via masking [90]. Yet, boat

815 noise can also act as a misleading cue and increase settlement of vessel hulls, because several

816 invertebrate species appear to mistake engine noise for coral reef soundscapes [91].

817 Once settled, animals may incur additional costs or benefits associated with sensory polluted

818 environments, which are going to define the intrinsic habitat quality of a location (HABITAT

819 QUALITY box). The three different mechanisms come with distinct costs and in some cases

820 distinct benefits, which we summarise in the bottom panel of the figure (see also main text:

821 "Linking Sensory Pollutants to Ecological Consequences"). In the case of benefits, such as

822 increased foraging opportunities in light polluted areas, animals may decide to stay (red

823 arrow) and even actively exploit sensory polluted environments, leading to an increase in

824 fitness (IMPACT ON FITNESS box). In the case of costs, animals may decide to stay and

825 cope via behavioural or physiological adjustments, leading to maintenance of or a reduction in

826 fitness. Alternatively, if the habitat is too degraded by sensory pollutants, animals may decide

827 to leave (red arrow) and search for more favorable habitats.

828 Previous experience with sensory polluted environments likely informs future habitat

829 selection and other life history stages and can thus lead to a cyclic pattern of habitat selection,

830 as shown in the figure. However, for many animals, habitat selection occurs without direct

831 experience in the optimal habitat – instead is driven by the evolutionary history of selection

832 on innate preferences and the refinement of these preferences via developmental plasticity [92].

833 For example, naïve bats use the echo-acoustic signature of water to select drinking habitat [93]

834 and this built-in perceptual bias attracts them to artificial structures with smooth surfaces.

835 Indeed, the bias is so strong that they are even attracted to vertical surfaces, such as large

836   glass windows of office buildings [94]. Polarized light is another hard-wired cue for selecting

837   oviposition sites in myriad aquatic insects and smooth anthropogenic surfaces such as

838   pavement can mislead these animals to lay their water-adapted eggs where they will soon

839   perish [95]. Understanding the mechanisms underlying animals' selection of sensory

840   environments is an important research frontier. This conceptual model is based on direct

841   effects only for sake of simplicity, although indirect effects, albeit complex, are also crucial to

842   understand [96]. Such indirect effects may often arise through changes in species interactions

843   (see main text: "Linking Sensory Pollutants to Ecological Consequences").

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846   **Box 2: Sensory danger zones**

847   The impact of a sensory pollutant may depend on its spatio-temporal overlap with the

848   distribution and activity of potentially vulnerable species. We thus define 'sensory danger

849   zones' as specific temporal windows or spatial areas in which such overlaps occur.

850   Crucial to this concept is the evidence that sensory pollutants vary in space and time.

851   We illustrate the concept of sensory danger zones in space and time with two examples: (a)

852   birdsong and the masking effect of noise, and (b & c) temporal overlap of noise and light with

853   animal activity at different latitudes. In the first example, songbirds are known to sing

854   predominantly at dawn. In temperate regions, dawn singing occurs mostly in early spring.

855   Depending on the latitude where a species occurs, the peak of dawn song may overlap with

856   the daily peak in traffic noise, the "rush hour", resulting in noise masking acoustic

857   communication between individual birds [61]. In this case the rush hour is the danger zone, but

858   only for birds that live close enough to roads to be subjected to the masking effect of noise [61].

859   However, in our example, such a danger zone disappears during the weekends, when the daily

860   peak in traffic noise occurs later and is not as intense as during the working days. In this case,

861   temporal speed restrictions might alleviate the effects of road noise on nearby ecological

862   communities. For our second example, the peak noise levels during the day never overlap

863   with light at night during the summer at high latitudes, as the days are long, and sunrise and

864   sunset occur much earlier and later than rush hour. In winter, however, there is a strong

865   overlap between light at night and traffic noise, because days are shorter and rush hour can

866   occur before and after sunrise and sunset, respectively. Thus, from a co-exposure perspective,

867   the danger zone is larger in winter than summer (b). In tropical regions, such a danger zone

868   might be present throughout the year, because there is little variation in photoperiod in

869 different seasons and peak traffic noise may occur during dark hours in the presence of light

870 pollution, especially in the evening (c).

871 Sensory pollutant levels also show strong spatial variation. Lower panels in the figure show

872 estimated anthropogenic noise levels (d), artificial light at night levels (e) as well as combined

873 levels of both pollutants (f). Most areas that receive high levels of artificial light at night also

874 receive high levels of anthropogenic noise. However, there is also considerable spatial

875 heterogeneity in exposure to noise, light or both. By taking advantage of existing variation in

876 co-exposure, as well as via experimental manipulations of these stimuli, future research can

877 begin to disentangle the effects of single sensory pollutants as well as to assess their combined

878 effects (additive, synergistic, antagonistic) [80].

879 Just as pollutants differ in their spatio-temporal distribution, species likewise differ in their

880 spatial and temporal activity. Indeed, most species can be classified as diurnal, nocturnal or

881 crepuscular. However, many others show considerable flexibility, often depending on external

882 environmental conditions, interspecific relationships or social factors [97,98]. For instance, a

883 recent meta-analysis highlighted how several mammalian species restrict their activity to

884 night in the face of intense anthropogenic activity, whereas in natural areas the same species

885 may be active during the day [99]. Species also differ in annual activity patterns [100]. For

886 instance, some species hibernate, while others are active throughout the winter. Such seasonal

887 changes in the activity of organisms are highly dependent on latitude, or on the environmental

888 gradients that are strongly correlated with latitude. Thus, species will differ in the exposure to

889 sensory pollutants they experience over the course of the day and year, based on their ecology

890 and geographic origin, leading to interspecific variability in sensory danger zones in time and

891 space.

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